ANNALS
OF
The Entomological Society of America

Volume XXIV JUNE, 1931 Number 2

PROFESSOR JOHN HENRY COMSTOCK*

February 24, 1849 — March 20, 1931

Professor Comstock was chairman of the committee on Organization of the Entomological Society of America; and at its first offical meeting in New York City on December 28, 1906, he was elected its first President.

If some of us still cherish the philosophy that a struggle for existence does act as a developmental factor, perhaps we shall be pardoned for believing that the early struggles of Professor John Henry Comstock for an education did develop in him some of those fit qualities that later contributed to his scientific achievements. Notwithstanding, something of his character must certainly be attributed to his parental inheritance. His mother, Susan Allen, was reputed to be of the family of Ethan Allen. Evidently it was she who transmitted to her son the determination and tenacity of purpose which characterized his labors on the problems he undertook to solve.

His father, Ebenezer Comstock, was a teacher who had spent two years at Williams College in Massachusetts. Apparently the father was a man of idealism and imagination. At any rate, he left the mother and the infant in Janesville, Wisconsin, where the latter had been born, and joined a party of "forty-niners" in search of the alluring, romantic metal, gold. Unfortunately his party became infected with cholera and he early succumbed to an attack of the disease. Thus the mother was left alone with a mortgaged farm which soon fell into unscrupulous hands and she lost it all. This accumulation of untoward events forced her to return with her son to her native state, New York. Here the struggle continued

*This account of Professor Comstock's life was written at the special request of the Editorial Board.

until finally she was forced to place the child in a public institution. Later, after passing short periods in the homes of different relatives, the boy accidentally found a genuine welcome to the home of Captain Lewis Turner, a retired sailor and a rigorously just but hospitable man.

"Here he was to have his board and clothes and three months schooling in the winter in return for which he was to do whatever work Captain Turner wished." The bargain was rigidly adhered to by both participants, but the boy was treated justly and kindly and for the first time within his memory he felt at home and happy. The three sons of Captain Turner were sailors on the Great Lakes and naturally when the boy Comstock reached the age of 16, he too became a sailor. This gave him an opportunity to earn enough money during the summer to defray the expense of attending school during the entire winter.

He had become interested in botany and had begun to search for a book which would give him some information regarding lichens and mosses. While his boat, on one of its cruises, was anchored in the port of Buffalo, he visited the shop of a book dealer in search of the desired work on Cryptogams. Instead of finding the botany he ran across that entomological classic, Harris' "Insects Injurious to Vegetation." The book with its fine plates interested him intensely and although he lacked the funds he determined to own it. He went to the Captain for an advance from his wages, obtained the necessary amount and the next day returned and purchased the precious book. The entry on the fly-leaf of this copy in Professor Comstock's own hand, made November 19, 1876, is as follows: "I purchased this book for ten dollars in Buffalo, N. Y., July 2, 1870. I think it was the first entomological work I ever saw. Before seeing it I had never given entomology a serious thought; from the time that I bought it I felt that I should like to make the study of insects my life's work." Undoubtedly this fortuitous event gave to entomology one of its masters.

By working summers and going to school winters he was ready at 20 years of age to enter that new institution, Cornell University, of which he had heard good report. He entered the University with the opening of its second year, in the fall of 1869. He literally helped to build the institution, for he

labored with his hands in the construction of McGraw Hall, the building in which he was later to become an instructor. The manner of his becoming an instructor is interesting. His knowledge of insects had already given him a reputation among his classmates; and in the spring of 1872, thirteen of them, including David Starr Jordan, petitioned the faculty to allow Comstock to give them a course in entomology. Thus he became an assistant, later an instructor, an assistant professor in 1876, and Professor of Entomology and Invertebrate Zoology in 1882, which position he held until his retirement in 1914, at the age of 65.

Although he entered Cornell in 1869, he became ill and had to defer his college education for another year. Entering again in the fall of 1870, this time to stay, he was graduated in 1874. During these early years he had been struggling by himself to gain a knowledge of entomology. But now that Agassiz had brought the European savant, Dr. H. A. Hagen, to Cambridge, Comstock while yet an undergraduate, embraced the opportunity to study with the latter during the summer of 1872. Professor Comstock has told the writer of his experience as a student with Dr. Hagen. The latter, a large man, would enter the laboratory in the morning, remove his coat, take a comfortable chair at a table covered with insect cases, light his large German pipe and say to Comstock, "Kom here und I vill dell you some dings vat I know aboot insects." To the young man filled with zeal for knowledge of his chosen field of work it was an inspiring and memorable summer.

During the year 1874–'75, Comstock spent some time in graduate work at Yale University giving particular attention to general invertebrate zoology. In 1888–'89 he was a student in the laboratory of Leuckart in Leipzig. His contact with Leuckart and with Leuckart's students exerted a most stimulating effect on his early career which lasted throughout his life. He returned to his work at Cornell with great enthusiasm and vigorous activity.

During the summer of 1878, C. V. Riley then chief entomologist of the United States Department of Agriculture, employed Comstock as temporary field agent. He was sent to Alabama to make a study of the cotton-leaf "worm" (*A. argillacea*). This was really his first extended work in the field of economic entomology. In the following April, 1879,

Riley resigned and Comstock was appointed to succeed him. For the following two years, Comstock, L. O. Howard, Theodor Pergande, and Mrs. Comstock with George Marx as illustrator, worked together in Washington harmoniously and most enthusiastically. It was during this period that Comstock made his basic studies on the Coccidæ. His reports for the year 1879 and the year 1880, together with his report on cotton insects, were also among the fruits of those two years. Soon after his return to Cornell University in 1881 he published his second report on scale insects. His interest in economic entomology continued through all of his active years.

His work as an investigator began to express itself in published papers as early as 1872. His ability and enthusiasm in research grew with the years. This is indicated by his papers on the Coccidæ (1880, 1883), his essay on The Descent of the Lepidoptera (1892), and on Evolution and Taxonomy (1893) and by his papers in collaboration with J. G. Needham on the wings of insects (1899). Subsequent papers embodying the results of researches on spiders appeared regularly during his later years. These culminated in the publication of "The Spider Book," (1912). Following his retirement in 1914 he devoted the remaining years to the rounding out of his life's work. The results of his long years of research on the wings of insects were finally brought together in the form of a book, "The Wings of Insects," (1918), probably his chief contribution of pure research. His last years were devoted to the writing of his final work, "An Introduction to Entomology." Happily this was completed before his last illness. Professor Comstock never engaged in controversy nor did he criticise the work of others. He did his own work as well as he knew how and with faith in it, passed over adverse criticism of it in silence. On the other hand, no one was franker to acknowledge a mistake than he, for accuracy was almost a fetish with him. Moreover, he never appropriated the work of others. Speaking of this just practice of his, Dr. Howard says, "Comstock was a very fair and honest man, as his subsequent career has shown."

Professor Comstock was one of the earliest teachers of entomology in the United States; and his ideals and standards have exerted a profound influence on the teaching of entomology in this country. His early struggles in self-education undoubtedly developed a mental tendency to obtain a clear, precise,

logical arrangement in his own mind of the problem in which he was interested. As a result, his lectures were models of simplicity, clearness, and conciseness. This logical quality of mind, together with his infectious enthusiasm and his personal interest in his students, made him a great teacher. Moreover this characteristic, together with his experience as a teacher, contributed to his success as a writer of text-books. His work as a teacher and organizer of the Department of Entomology at Cornell led David Starr Jordan, of Leland Stanford Jr. University, to invite him to organize a similar department at that University. Accordingly his winter vacations from 1891 to 1900 were spent at Stanford where, with Dr. Vernon L. Kellogg, he organized and conducted the work in entomology on much the same basis as at Cornell.

The summer season at Ithaca has always been an ideal time for the study of insect life. The diversity of topography in the Finger Lakes region together with the accompanying variations in climatic features provides a wide variety of flora with a great diversity of insect fauna. During the summers for many years, Professor Comstock offered instruction in entomology at Cornell for a term of ten weeks. The usual daily procedure was to gather at 8 a. m. in the lecture room and listen to a clear, concise account by Professor Comstock of the habits and characteristics of a group of insect forms. The lectures followed the order and arrangement of the material as outlined in the well-known "Manual for the Study of Insects." At the close of the lecture, everyone equipped with collecting apparatus, went into the field for the remaining part of the forenoon. In the afternoon the collected specimens were mounted, studied and determined as far as possible. Thus each student became acquainted with a wide range of forms, with their habitats, often with their food plants and finally with the literature treating of them. It was during these summer terms that many of Professor Comstock's older, more mature students came to Ithaca to pursue advanced work in entomology. It has seemed to the writer that those summer seasons of laboratory and field instruction offered nearly ideal opportunities for acquiring a basic knowledge of insect life. It was during the latter part of this period of Professor Comstock's career that he became more deeply interested in morphology and began the development of that phase of entomology

in his laboratories. Professor Comstock never stagnated in his own growth or in the growth of his department. During the years of his labors he taught entomology to more than 5,000 students. Certainly all of these especially interested in entomology participated in the hospitality of the Comstock home. Indeed, Professor and Mrs. Comstock always maintained an open house for students of the University; and the cordial warmth of sympathy and hospitality enjoyed in their home will remain a precious memory to scores of men and women all over the world.

Professor Comstock was so absorbed in his work as teacher and investigator that he gave little time or thought to the more public activities of scientific societies and organizations. His devotion to his students, his zeal to advance the science of entomology, his loyalty to Cornell University and his ardor to enchance its prestige, animated his life with a great, single, unselfish purpose. His quiet, effective achievements have received wide recognition. On his retirement his students presented a memorial to him in the form of a generous fund, the income from which is devoted to the upbuilding of a "Comstock Memorial Library" of entomology. He was an honorary member of the Entomological Society of London; an honorary member of the Entomological Society of the Netherlands; a member of the Entomological Society of France; of the American Philosophical Society and of the California Academy of Sciences. He was made an honorary member of the Fourth International Congress of Entomology. His books are known and used the world over. Goldwin Smith, an early teacher of history at Cornell, inspired us with the moral principle that above everything is humanity. Accepting this, we may well believe that Professor Comstock's greatest memorial consists of that splendid body of men and women who have gone out under his training and inspiration to hand on the truth as he tried to teach it.

On the night of Thursday, March 19, 1931, he suffered a final collapse and during the early morning of Friday, March 20, he succumbed. On the following Tuesday his ashes were placed beside those of Mrs. Comstock in Lakeview Cemetery on a beautiful site overlooking the valley and Lake Cayuga. Thus he lived and completed a life devoted to his science, to his students and friends, to his beloved Alma Mater and to an unselfish effort to promote useful and cultural knowledge.

GLENN W. HERRICK.

A STUDY OF THE GENUS NEMOBIUS. (ORTHOPTERA: GRYLLIDÆ).*

B. B. Fulton,
North Carolina State College.

The genus *Nemobius* is one of the largest of the family Gryllidæ and has world-wide distribution. The most comprehensive work on the American species of the genus is a revision by Hebard (1) which cleared up the synonymy and made it possible to identify the species with greater assurance. His classification is based largely on the characters of the ovipositor, for few reliable male characters were known at that time.

In studying the mating habits of these crickets, the writer discovered that the concealed genital armatures of the males which are protruded while mating provide excellent characters for the identification of most of the species. A study of their structure throws further light on the relationship of our native species. While they do not clearly differentiate races or some closely related species, they make it possible to identify several species with greater certainty with the male sex than with the female.

In order to point out some of the important male characters it is necessary to describe the genetalia and originate some terms for the rigid parts of a protrusible organ that is described more fully in connection with the mating habits. When not in use this organ lies in a horizontal position above and concealed by the subgenital plate. In recently killed specimens, it can easily be pulled out by an insect pin with a slightly bent point, which can be hooked on to the basal supporting structure. On drying, there is a tendency for the organ to pull back into the body unless the attached membrane has been greatly stretched or ruptured. This does not apply to specimens which have been previously dried and relaxed.

The entire structure is roughly cylindrical in shape. The basal part of the dorsal† face, is the main supporting structure.

*Published with the approval of the Director of Research as paper No. 44 of the journal series.

†All terms of orientation in the discussion of this structure apply to the horizontal position assumed when withdrawn into the body.

The attached lateral pieces may be termed claspers since they are provided with muscles that draw the ventral edges together. The ventral face is hollowed to form a longitudinal

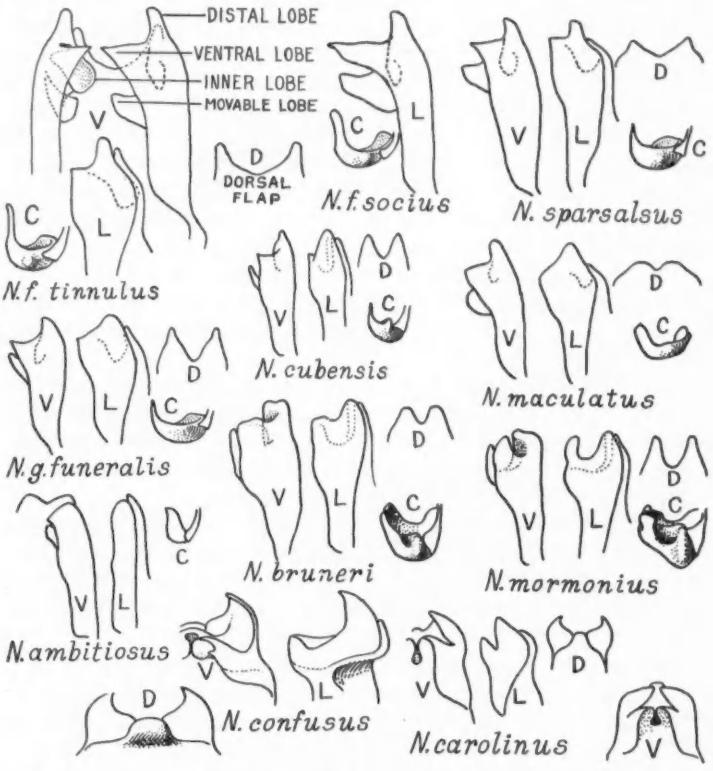


FIG. 1. Male genitalia: right claspers and dorsal flaps. V, Ventral view. L, Lateral view. C, Caudal view. Ventral view of *tinnulus* is of both claspers from a slightly lateral position to show inner lobe of the left. Inner lobes in other ventral and lateral views, indicated by dotted lines.

groove between the claspers. At the distal extremity each clasper is hollowed out on the mesal or internal face and in most of the species has a distal lobe, a ventral lobe which in some species is a sharp tooth, an inner lobe on the mesal face and a movable lobe which is rather loosely attached to the mesal surface, proximad to the inner lobe. The distal extension of

the main supporting structure on the dorsal side fills in the space between claspers on that side and may be called the dorsal flap. The outline of its distal margin furnishes important specific characters.

The ventral groove is provided with thick cuticle, which retains its shape, but between that and the bases of the claspers are areas of thin integument which collapse on drying. The extent to which the claspers are drawn together will affect their appearance and often the internal and movable lobes are hidden. For this reason the ventral and lateral views of the claspers shown in Fig. 1 are drawn from an arbitrary position as if the tips of the ventral lobes did not quite reach the median line although in many specimens they will be found to overlap considerably or may be widely separated.

RELATIONSHIP OF THE SPECIES

The characters of the male genitalia substantiate with few exceptions, Hebard's grouping of species found in the United States. No specimens were available for examination of *Nemobius carolinus brevicaudus* Bruner, *N. carolinus neomexicanus* Scudder and *N. eurynotus* Rehn & Hebard.

Those species having the disto-ventral spurs of the caudal tibiæ equal in length; namely, *carolinus* Scudder and *confusus* Blatchley have a distinct type of male genitalia. The claspers are very short and are attached diagonally to the dorsal support. The distal lobe is hollowed on the mesal face and is claw-like in shape. The ventral lobe is also claw-shaped but attached to a fold of thin integument which meets the one on the opposite side forming a diaphragm in the ventral groove. This fold, apparently, takes the place of the movable lobe in the other species. The dorsal flap is reduced to a small, rounded, arched extension of the dorsal support.

Among the species having unequal disto-ventral spurs on the hind tibiæ, *N. ambitiosus* Scudder seems to stand in a class by itself. It has a unique feature which was called to the writer's attention by A. N. Caudell, of having a bald shining face. The bristles of the head are limited to the occiput, while in other species they reach as far as the median ocellus. The male claspers lack distinct distal and inner lobes, but have the usual form of movable lobe. The dorsal flap is long and has a very shallow median notch.

Of the remaining species, those having the longer and straighter ovipositors, namely, *fasciatus* (4 races), *griseus* (2 races), *sparsalsus* Fulton and *maculatus* Blatchley, have a common feature in the male sex in the shape of the inner lobe of the clasper which is difficult to see without dissection. This is flattened and concave on the mesal face; and extends dorsocephalad beneath the dorsal flap. In *maculatus*, it is reduced to a small projection on dorsal edge of the clasper, and this species differs further in having blunt ventral lobes on the clasper, and a short rounded dorsal flap with a small rounded median notch.

The male genitalia of *N. griseus griseus* E. M. Walker and *N. grieseus funeralis* Hart are very much alike, and are characterized by the broadly rounded distal lobe of the clasper, when viewed from the side. The clasper of *sparsalsus* has a very broad base and short ventral lobe. The dorsal flap has a very shallow notch, and the lateral angles are not prolonged. The genitalia of the races of *fasciatus* are described under the discussion of that group.

Among the species with short ovipositors, *cubensis* Saussure, *palustris* Blatchley, *bruneri* Hebard and *mormonius* Scudder, the dorsal edge of the inner lobe of the clasper takes the form of a prominent longitudinal ridge on the mesal face, extending directly cephalad from the distal lobe. *Cubensis* and *palustris* have almost identical male genitalia. In specimens of *palustris* examined the dorsal edge of the inner lobe was more prominent and extended more nearly to the tip of the distal lobe than is shown in the ventral drawing of the clasper of *cubensis*. In both species the ventral lobe is very thin and sometimes bends inward on drying.

The male genitalia of *bruneri* and *mormonius* show similarities but are distinct enough not to be confused. Both have the movable lobes very narrow at the tips where they are parallel to the mesal edges of the ventral lobes. At the base the movable lobes are thin walled and extend across the mesal faces of claspers forming a diaphragm. In this they are supplemented by the cephalic end of the inner lobe of the clasper which curves sharply around to the ventral side and partly closes off the space between the two claspers, caudad to the basal portions of the movable lobes.

In *mormonius* the notch between the ventral lobe and the distal lobe is very deep, the inner lobe forms a large part of the above described diaphragm and the cephalic margin extends to the base of the ventral lobe. The dorsal flap has narrower lobes and a deeper notch than in *bruneri*. In *bruneri* the cephalic edge of the inner lobe is not prominent and it recurves almost to the apex of the ventral lobe.

It is evident that *mormonius* is a distinct species showing closest relationship to *bruneri* and not a geographical race of *cubensis* as formerly considered. My specimens from the Bright Angel Trail of the Grand Canyon, Arizona and two male specimens from Las Vegas, Nev. loaned by Hebard belong to the same species. The male allotype of *mormonius* designated by Hebard was from Las Vegas. The designated type was from St. George, Utah. The two localities are only a little over a hundred miles apart and both in the Colorado basin so it is unlikely that the female would be a different species. The specimens examined have a pale face with a faint trace of a pattern similar to the dark pattern found in *bruneri*. There is a darker band across the occiput from eye to eye. This is present in *bruneri* but is broader and does not quite reach the eyes. The pronotum has a pattern similar to *bruneri* but with less contrast in the colors. The legs also lack conspicuous markings.

Two male specimens from Brownsville and Dickinson, Texas, loaned by Hebard as specimens of *mormonius* have the genitalia as in *bruneri* although the coloration is more like *mormonius*. The placement of these specimens involves the relative specific value of color characters as against the morphological characters of the male genitalia. I prefer to depend on the latter for in other species covering a wide geographical range there is little variation in their structure.

The determination of the geographical limits of *bruneri* and *mormonius* and the relationship of the two species will require a study of the male genitalia of a large number of specimens.† Hebard (1) pointed out the resemblance to *bruneri* of the Texas specimens he placed under *cubenses mormonius*. Further

†Since writing this paper the writer has examined specimens, loaned by Hebard, from localities ranging from Beauregard Co., La., to Brownsville and Del Rio, Texas, all of which were similar to the above mentioned Texas specimens in coloration and genital structures.

study may show that they comprise a geographical race of *bruneri* or that they are a connecting link between *bruneri* and *mormonius*.

THE RACES OF N. FASCIATUS

This species seems to be in the process of splitting up into races which are not well defined morphologically but are definite entities in nature. Three of the races have been recognized and named. The fourth has apparently escaped description as a new species or variety by earlier entomologists, while both typical *fasciatus* and the race *socius* are credited with more than one synonym. This is explained by the more secretive habits of the race, resulting in fewer specimens in collections. In order to give this race a name for further discussion of the problem it is here defined as a new subspecies.

*Nemobius fasciatus tinnulus** new subspecies. Type; male; Raleigh, N. C., September 16, 1928. Types to be deposited in the U. S. National Museum.

Nemobius fasciatus tinnulus subsp. nov.

A male was selected for the type because that sex presents more characters to distinguish it from the other races of *fasciatus*. It differs in the following features: dorsal field of tegmen relatively broader, (Fig. 2, A); in life the lateral margins of dorsal fields held nearly parallel; longitudinal or proximal portion of stridulatory vein forms nearly a right angle with the file; length of the file, as far as the perpendicular branch on the distal side (1.5 mm.) greater than the remaining portion of the lateral field (1.2 mm.); distal margin of dorsal field broadly rounded; length of exposed dorsal field 5.4 mm.; greatest width 2.9 mm. Allotype; female; same data as type.

Length of ovipositor as far as perpendicular portion of base on dorsal side, 7.5 mm.; length to extreme base on ventral side, 7.9 mm.; length of hind femur, 7.5 mm. Tip of ovipositor with 9 teeth on dorsal margin; toothed margin with a slight curvature, (Fig. 2, D). Color notes: By comparison with Ridgway's "Color Standards and Nomenclatures," the ground color of the head above the median ocellus is close to orange cinnamon; an obscure pattern between the upper portions of the eyes, snuff brown; face below ocellus kaiser brown; pronotum snuff brown, slightly darker on dorsal portions of lateral lobes, ventral portion of lateral lobes cinnamon buff; legs and ventral side of body with a ground color of cinnamon buff, but on the legs almost entirely obscured by buffy brown; on the hind femur the brown is in the form of numerous oblique dashes. In the male the sides and

*Tinnulus = Tinkling, clinking. So named because of the quality of the song.

dorsum of abdomen nearly entirely black. In the female, concealed portion black; exposed portion buffy brown with a rather broad black median stripe; sides with large black patterns on the cephalic portions of the segments; lateral portions of dorsum with two small black spots on each side near the caudal border of each segment.

The male tegmina are darkly infuscated over the areas shaded in the illustration, (Fig. 2, A). Paratypes selected; 1 male, 1 female, same data as type; 1 male, 2 females, Raleigh,

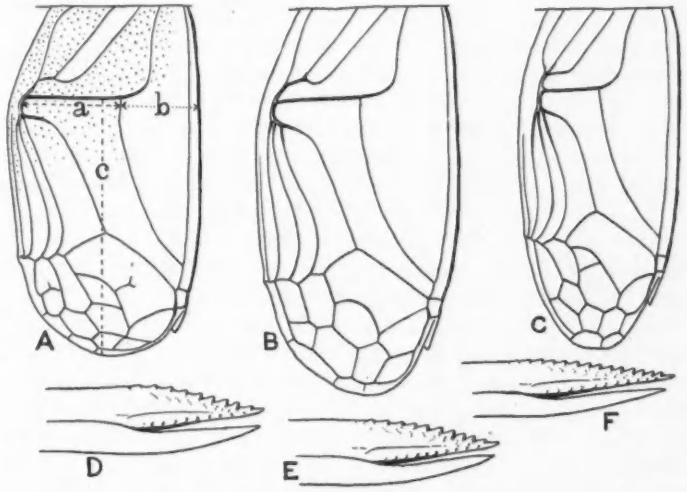


FIG. 2. Tips of ovipositors and male tegmina. A, *N. fasciatus tinnulus*, type. D, *N. fasciatus tinnulus*, allotype. B. E., *N. fasciatus fasciatus*, (Raleigh, N. C.). C. F., *N. fasciatus socius*, (Raleigh, N. C.).

October 8, 1928; 1 male, 1 female, Raleigh, October 15, 1930; 1 male, 1 female, Plymouth, N. C., October 25, 1928.

This woodland race was first observed at Mt. Pleasant, Iowa, where it attracted the writer's attention by its characteristic type of song. It was not found in any other part of Iowa. At that time it was regarded as a purely physiological race of *fasciatus* and its habits were commented on in an earlier publication (2). In North Carolina it is common in woods over a large part of the state. In addition to the localities represented by the paratypes, it has been taken in N. C. at Reidsville, in the north central portion and at Sparta and

Burnsville in the mountain regions. In the U. S. National Museum, specimens from Falls Church, Va. (A. N. Caudell) and Thompsons Mills, Ga. (H. A. Allard) appear to belong to this race.

The subspecies *tinnulus* represents one extreme in the evolution of the *fasciatus* (De Geer) group with *socius* Scudder as the other extreme. The race *abortivus* Caudell from the northern prairie regions seems to be an offshoot in another direction toward *N. griseus*. After studying the races *tinnulus*, *fasciatus* and *socius* in Iowa and North Carolina, both in the field and the laboratory, the writer has formed a different conception of them than that of geographical races based on the relative length of the ovipositor and hind femur. It is true that *socius* in the southern states where it is the commonest race has a relatively short ovipositor but in northern grass marshes there exists a form which is similar to *socius* in habits and in appearance, with the exception of the ovipositor length. The woodland specimens from Mt. Pleasant, Iowa which I am referring to *tinnulus* also have longer ovipositors than the southern specimens but they agree in other characters and in habits. On the other hand, I have recently found in restricted environment near Raleigh, crickets which have as long ovipositors as *fasciatus* in the north and which have other morphological characters and song habits agreeing with that race. The problem is complicated by the fact that the above crickets which appear to be *fasciatus* have a very restricted habitat while in the north, it is the most widely distributed race. In North Carolina, *socius* is widely distributed and tolerates a rather wide range of environmental conditions while the cricket in the north that resembles it has a restricted environmental range.

If we are to recognize any subspecies of *fasciatus* we have at present two choices for the basis of separation. The first is the single female character of relative ovipositor length which offers no more clear cut line of demarkation than any of the characters in the second choice and leaves in both groups physiologically distinct races. The second choice is a combination of characters including the shape of the male tegmen and the relative proportions of some of its areas, the number of teeth in the stridulatory vein, slight differences in the tip of the ovipositor, and some differences in coloration applicable to

both sexes. These differences are correlated with physiological differences recognizable in song habits, seasonal history and in the choice of environment. The above characters are not a direct result of environmental influence for all races have been bred from the nymph in the laboratory under identical conditions and all remain true to type both in structural characters and song. Also in certain border line areas two races may be found intermingled but apparently not intergrading. There appears to be inherent differences between the races which cause them to choose different environments.

My studies have led me to place greater confidence in the second basis of separation as outlined above and to consider the subspecies of *fasciatus* as ecological races rather than geographical. This conception greatly extends the recognized range of *socius*. It is admitted that the characters described below will not suffice to place many specimens from a miscellaneous collection into one of the three subspecies. But neither can this be done on the relative length of the ovipositor. The advantage of the geographical conception of the subspecies is that they can be classified by the locality labels. If locality labels also bore ecological data, they would help in the same way with my classification. Thus it is apparent that certain song and habitat differences noted by Allard (3) in Mass. are those of the races *fasciatus* and *socius*.

I believe that the three subspecies are physiologically distinct and that any individual belongs to one of the three, but that morphologically they have not diverged far enough to make exact classification possible. For this reason I see no reason why any of these crickets should not be referred to merely as *Nemobius fasciatus* in any general discussion where fine distinctions are not involved.

The following outline of racial characters will aid in determination of the subspecies. With a series of specimens taken from a single type of habitat the average condition found will probably indicate the race.

Male right tegmen: Spaces mentioned are shown in Fig. 2, A. Space a, length of stridulatory vein between the crest of the vein which it joins at the inner margin and the perpendicular branch near the middle. Space b, from the above mentioned branch to the outer margin of the dorsal

field. Space c, from the stridulatory vein to tip. Measurements of the extremes in millimeters.

No. of Specimens	Locality	space a	space b	space c	a minus b (algebraic)
	Tinnulus.				
8	Raleigh, N. C.....	1.3 to 1.5	1.1 to 1.3	3.4 to 3.9	.1 to .3
5	Mt. Pleasant, Iowa	1.3 to 1.5	1.2 to 1.4	3.6 to 4.2	0 to .3
7	Reidsville, N. C...	1.2 to 1.4	1.2 to 1.3	3.5 to 4.	0 to .1
	Fasciatus.				
8	Iowa, (mostly from Ames).....	1.1 to 1.2	1.0 to 1.3	3.4 to 4.2	—.1 to .2
12	Raleigh, N. C.....	1.3 to 1.4	1.3 to 1.5	3.8 to 4.4	—.2 to 0
3	Burnsville, N. C...	1.0 to 1.3	1.1 to 1.2	3. to 3.5	—.1 to .1
	Socius.				
20	Raleigh, N. C.....	.7 to 1.0	.9 to 1.3	2.8 to 4.2	—.4 to —.1
8	Ames, Iowa.....	.7 to 1.0	1.0 to 1.3	3. to 3.8	—.3 to —.1
4	Geneva, N. Y.....	.8 to .9	1.1 to 1.2	3.3 to 4.	—.4 to —.2
5	Chadbourne, N. C.	.8 to 1.0	1.1 to 1.3	3.4 to 3.8	—.4 to —.2
6	Phelps Lake, N. C.	.8 to .9	1.0 to 1.2	3.2 to 3.8	—.4 to —.2
5	Fort Collins, Colo..	.8 to .9	1.2	3.3 to 3.5	—.4 to —.3
7	Albuquerque, N.M.	.9 to 1.1	1.2 to 1.4	3.4 to 4.2	—.4 to —.2

The male tegmina in *tinnulus* are generally large compared to the size of the body although only wingless forms have been found. In *socius* the tegmina are relatively smaller except in the macropterous forms which are sometimes found. In the former race, the tegmina are broader in comparison to the length and the tips are more broadly rounded. The tegmina of *fasciatus* are intermediate in all respects. Winged forms of the last race also occur.

The number of teeth in the stridulatory file varies considerably between the three races. Unfortunately, this cannot be determined without removing one of the tegmina and mounting it on a slide for examination under high magnification. There seems to be some variation within each race, correlated with size of tegmen, but a very small *tinnulus* has more teeth in the file than a very large *socius*. Counts made of various specimens are as follows:

Tinnulus—Raleigh, N. C., 228, 239; Sparta, N. C. (smallest, exposed portion 3.4 mm.) 187; Mt. Pleasant, Iowa, 208.

Fasciatus—Ames, Iowa, 185, 197; Grandfather Mtn., N. C. (small, 4.6 mm.), 184; Raleigh, N. C. (largest, 6 mm.), 192, 194.

Socius—Raleigh, N. C., 105, 129, 145, (smallest) 115; (largest) 140; Ames, Iowa, 113, 117, 126; Geneva, N. Y., 127, 139.

Typical examples of the male claspers of *tinnulus* and *socius* are shown in Fig. 1. The greatest difference is in the ventral lobe which is acutely pointed in the former and rounded in the latter. In *fasciatus* an intermediate condition is found. There is some variation in all three races so that the character is of no greater diagnostic value than the others mentioned.

The table below gives the measurements of the ovipositor (dorsal edge to expanded basal portion), hind femur, and the individual difference of the first minus the second, expressed as minus quantity when the femur is longer than the ovipositor.

No. of Specimens	Locality	Ovipositor	Femur	Ovipositor minus Femur (algebraic)
	Tinnulus.			
10	Raleigh, N. C.	6.2 to 7.8	6.2 to 7.6	—.6 to .6
6	Reidsville, N. C.	7.0 to 7.8	6.8 to 7.8	—.2 to .7
4	Sparta, N. C.	6.4 to 8.1	5.4 to 6.8	.9 to 1.7
3	Mt. Pleasant, Iowa	7.6 to 8.8	7.3 to 7.7	0 to 1.3
	Fasciatus.			
18	Ames, Iowa	6.2 to 8.2	6.4 to 7.6	—.6 to 1.4
8	Mt. Pleasant, Iowa	7.0 to 9.0	6.6 to 8.2	0 to .8
6	Pointe au Baril, Ont	8.0 to 9.1	6.5 to 7.0	1.0 to 2.5
7	Burnsville, N. C.	6.2 to 7.2	5.7 to 6.6	.2 to .8
26	Raleigh, N. C.	7.8 to 9.4	7.2 to 8.8	0 to 1.0
	Socius.			
29	Ames, Iowa	6.4 to 8.6	6.1 to 7.8	—.2 to 1.0
12	Sparta, N. C.	5.8 to 7.8	6.2 to 7.4	—.4 to .7
21	Raleigh, N. C.	5.2 to 7.4	5.8 to 7.6	—.7 to 0

The above figures show that there is no correlation between relative length of ovipositor and hind femur, and the races as here defined. Considered geographically, there is some correlation but there is so much variation in one locality that the extremes greatly overlap. Thus by lumping all specimens from Raleigh, N. C. and all from Iowa we would get a range of −.7 to 1.0 for Raleigh and −.6 to 1.4 for Iowa.

In the shape of the tip of the ovipositor there is a slight difference between the races, typical examples of which are shown in Fig. 2. In *tinnulus* and *fasciatus* there is a slight curve to the dorsal outline of the toothed portion, intensified by the fact that there is a considerable increase in the size of the teeth toward the tip. There are usually 8 or 9 teeth visible in profile in *tinnulus*, 9 or 10 in *fasciatus* and 11 to 13

in *socius*. In the last the toothed portion is straight and none of the teeth are very large. These characters are often destroyed by the use of the ovipositor. In many specimens all of the teeth have been worn completely away.

The coloration of all three races varies so much that little dependence can be placed on it as a character. On the average *tinnulus* is more tawny. The head is pale or dark reddish brown but in either case the dark markings, if present at all, are inconspicuous. The face below the median ocellus is only slightly darker than above, if at all. The dorsum of the pronotum is more uniform in color and usually pale, but if dark, the lateral portions are only slightly paler and not conspicuous stripes. In *fasciatus* the usual color is dull brown to nearly black with head markings and lateral stripe on dorsum of pronotum more distinct. The face below the median ocellus is usually considerably darker than the ground color above. In *socius* the color is often almost entirely black but if paler, the markings are quite contrasted. The head stripes may be reduced but usually they are black and the face below the ocellus is often black. The dorsum of the pronotum is generally dark or black with distinct buffy lateral stripes. The dorsum of the exposed abdominal segments in pale specimens has a continuous pale median line bounded by black lines while light specimens of the other two races have the median line black with at most a pale median dot at the caudal border of each segment. This difference applies to the whole abdomen in nymphs.

SEASONAL HISTORY.

The seasonal history of *socius* at least in the Piedmont and Coastal Plain of North Carolina differs from that of *tinnulus*. The former begins to mature before the middle of June, and small nymphs of a second generation appear in the latter half of July. In the laboratory nymphs hatched out within two weeks after adults had been placed in a cage. Nymphs may be found until late fall and it is entirely possible that there may be a partial third generation. No adults have been found of *tinnulus* until after the first of August in the past two years. There is no evidence of more than one generation. No observations have been made on the seasonal history of *fasciatus* in this region for it was not discovered here until the

middle of October, 1930. In Iowa the earliest record I have for adults of *socius* is July 5, 1926 and for *fasciatus* August 3 of the same year but no effort was made to determine the earliest appearances. On August 1, 1929 near Pomeroy, Ohio an effort was made to find all three races but *socius* was the only one that could be heard singing.

After *socius* the earliest species to mature in N. C. are *carolinus*, *cubensis*, and *funeralis*. Adults of all three may be found at Raleigh about the first of July. In the southeastern part of North Carolina adults of *carolinus* and *cubensis* were found on June 22. All three species probably have more than one generation during the summer. Near Raleigh adults of *confusus* have been taken as early as July 29 but none of *palustris* earlier than August 12 at which time there were many still immature. The earliest catch of *bruneri* is September 10 but at that time only a few nymphs were present.

CROSSING EXPERIMENTS.

At the borders of woods, *tinnulus* and *socius* are sometimes found intermingled over very limited areas. Some experiments were performed to see whether they might mate with each other. Female nymphs of both kinds were collected and kept in cages until maturity. Then they were caged with males as outlined in the table below. After a number of days the females were killed and the seminal receptacles dissected out. When filled with sperms the receptacle is distended and glistening white, otherwise it is collapsed and translucent. All unfilled ones were examined under high magnification to see if any sperms were present.

In the five experiments where the crickets were caged with their own kind seminal receptacles were completely filled. Of the seven experiments where they were caged with another race only, two showed no traces of sperms in the receptacle. In three of the four experiments where the male was caged with females of both kinds, the receptacle of the female of different race showed no trace of sperms and in the fourth, only a few, as if from one mating.

In two larger cages several females of each race were placed with males of the other race. The cages were kept in a screened insectary over winter and the soil watered occasionally. No

offspring were obtained the following summer. No check was run with crickets mated with their own race so the results are entirely negative.

Females	Males	Number of Days Together	Condition of Seminal Receptacle
Tinnulus	Tinnulus	13	Filled.
Tinnulus	Tinnulus	8	Filled.
Tinnulus	Tinnulus	14	Filled.
Tinnulus	Tinnulus	14	Filled.
Socius	Socius	24	Filled.
Tinnulus	Socius	8	Filled.
Tinnulus	Socius	18	Empty.
Tinnulus	Socius	18	Filled.
Tinnulus	Socius	18	Filled.
Tinnulus	Socius	14	Empty.
Socius	Tinnulus	37	Filled.
Socius	Tinnulus	37	Filled.
Socius and Tinnulus	Socius	6	Socius filled; Tinnulus empty.
Socius and Tinnulus	Socius	24	Socius filled; Tinnulus empty.
Socius and Tinnulus	Tinnulus	6	Socius empty; Tinnulus filled.
Socius and Tinnulus	Tinnulus	24	Socius with few sperms; Tinnulus filled.

During the summer of 1930 similar experiments were run with the addition of *fasciatus* from the mountains. All three races have been caged with their own kind and the two other races. They have been kept in large glass jars with previously heated sand and soil in the bottoms. No offspring appeared during the fall so the jars will be kept at outdoor temperatures until spring.

MACROPTEROUS FORMS.

Individuals with long hind wings greatly exceeding the tegmina have been found in the following species: *fasciatus fasciatus*, *fasciatus socius*, *griseus griseus*, *griseus funeralis*, *cubensis*, *carolinus* and *mormonius*. Blatchley's (4) record of a macropterous specimen of the last species from Yuma, California is probably correct but the Texas macropterous specimens mentioned by Hebard (1) may prove to be *bruneri* if the

male genitalia are examined. The macropterous individuals are often attracted to lights at night in large numbers. They probably serve to disseminate the species.

In looking through collections, it was noticed that there are some individuals both male and female, with longer tegmina but without wings. An examination of some of these specimens showed that they do not have the usual vestigial wings but that the wings have been broken off at the base. They have a peculiar development of the metanotum and first abdominal tergite which is found only in macropterous forms. (Fig. 3.)

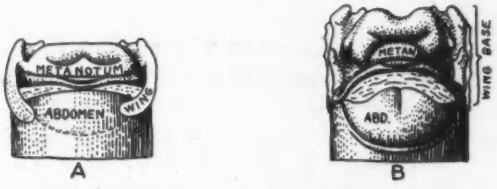


FIG. 3. Metanotum and first abdominal tergite of (A) micropterous form and (B) macropterous form with wings broken off.

This summer I had placed a macropterous *fasciatus* male with a female in a cage. A few days later the male had no wings and there was no trace of them in the cage. I thought that the female had probably chewed them off. The next macropterous individual that I found, which happened to be a male *funeralis*, I placed by itself in a cage. The next day it had no trace of wings and they could not be found in the cage. It must have broken them off in some way and devoured them. It seems reasonable to conclude from these observations that the wings of macropterous forms are not kept throughout their life and that such individuals settle down to an earthly existence, possibly after having migrated to new territory.

SONG HABITS.

The males of the genus *Nemobius* are persistent singers both by day and night. Their songs are neither very loud nor of very musical quality. With the exception of two species which sing alike all have characteristic types of song which can be recognized in the field by anyone who has learned their peculiarities. The best way to study the song habits is to

cage a few pairs where they will be away from the confusion of other insect sounds. In this way I have learned the songs of all the eastern species with the exception of *N. griseus griseus* E. M. Walker.

In recording the peculiarities of an insect song for the purpose of identifying it later in the field, the most important feature is the time element, which can be measured with greater accuracy than pitch, tone quality or loudness. The songs of various species of insects present so much diversity in length and frequency of notes, meter and rhythm that only modifications caused by extremes in temperature are apt to confuse them.

The question may arise as to why anyone should want to recognize the song of a *Nemobius* or any other insect. It may be for the same reason that many people learn the songs of birds, simply for the pleasure of knowing what causes the sounds. Another reason is that this knowledge facilitates the study of interesting problems in ecological distribution, by enabling the investigator to know where the various species live without the difficult task of finding them. From the collector's standpoint there is the added value that rare species may be located by tracking down the unusual song.

When singing the male *Nemobius* raises the tegmina to about a forty-five degree angle with the body and spreads them apart a little. They are then vibrated in a transverse direction. As with most crickets the right tegmen in *Nemobius* is always uppermost. The two tegmina are not identical. The right is slightly more infuscated and has a rougher surface. The left only has a narrow bead or raised edge on the inner margin where it comes in contact with the stridulatory vein of the right. Both have a well developed file or series of minute transverse ridges on the under surface of the stridulatory vein.

Several species of Nemobius produce more than one type of notes. One type which may be termed the calling song is produced when the male is alone or not sexually excited and is the one most frequently heard. The other which I have termed the mating song is used when the male is actively courting the female. During this song he is generally facing the female and puts on something akin to a dance by jerking the body backward and forward in time with the sounding of the notes. If the female departs during this performance he will

again resume the calling song. Old males often have a weak song as if the file had become worn with use.

The following key applies to the calling songs at temperatures of 70° F. or higher:

I. Made up of repeated short notes never much over a second in length and never so rapid but that the individual notes can be plainly heard.
  1. Sharp metallic chirps, with constant rhythm, 6 to 9 per second.
    N. fasciatus tinnulus n. subspecies.
  2. Notes of rougher quality, observable variations in rhythm, 3 to 7 per second.
    N. fasciatus socius Scudder.
  3. Longer notes, one-half to one second in length.
    a. Non-rhythmical, occasional notes 2 to 3 seconds long.
      N. sparsalsus Fulton.
    b. Rhythmical but not very constant, notes of more uniform length.
      N. ambitiosus Scudder.
    c. Each note begins as a low buzz with two undulations, audible only a few feet away, then increases in volume to the end, intervals between notes bery brief; rhythmical, but not constant.
      N. confusus Blatchley.

II. Sound continuous for several seconds at a time.
  1. Notes and rests of about equal duration, usually 5 to 15 seconds.
    N. cubensis Saussure.
    N. palustris Blatchley.
    N. palustris aurantius R. and H.
  2. Song interrupted at irregular intervals, usually 5 to 10 seconds, by breaks of less than a second duration.
    N. griseus funeralis Hart.

III. Song usually continued for indefinite period.
  1. Of shrill tinkling quality without modulations.
    a. With evident tremolo; at lower temperature song becomes a rapid series of sharp chirps, but at summer temperatures these are at a rate estimated at 12 to 15 per second.
      N. fasciatus fasciatus (De Geer).
    b. A thin high pitched sound with a tremolo so rapid that it can scarcely be detected at summer temperature.
      N. bruneri Hebard.
  2. With modulations.
    a. A weak tinkling sound with regular rhythmical undulations 5 to 7 per second.
      N. maculatus Blatchley.
    b. With a droning quality, variable in volume, part of the time louder and with rapid undulations, at other times weaker, lower pitched, without undulations.
      N. carolinus Scudder.

The song of *N. fasciatus fasciatus* is one of the loudest in the genus. The calling song is a continuous high pitched tinkling metallic sound. One can imagine that it might be produced by a small bell attached to the end of a length of spring steel that vibrates with about 10 to 15 swings per second. The sound is actually a series of short distinct chirps but at 80° F. or above this quality can scarcely be recognized. On cool days the chirps are plainly apparent and can be estimated

by tapping a paper with a pencil point at as near the same rate as possible for a period of a few seconds moving the pencil along so that the dots can be counted and the number per second computed. Estimates were thus made of Iowa specimens at 50° F., between 5 and 6 chirps per second, at 61° F., about 8 or 9. Specimens from North Carolina mountains chirped close to 7 times per second at 60° F., at least 8 per second at 66° F. and over 9 per second at 68° F. Specimens from Raleigh, N. C. appear to have a slightly higher rate than the mountain specimens.

In watching a male singing it appears as if each chirp were produced by a single movement of the tegmina. The movement is too rapid to be visible. The tegmina seem to be held motionless at the outer limit of the swing indicating that they must be held stationary in this position for a brief period between each stroke.

There are two variations of the mating song. When a male is facing a female it sometimes sings as described above in short phrases about one and one-half to three seconds duration, with rests of about half a second. At other times the male chirps louder and at much slower rate, about 5 to 6 per second, without regular rhythm and accompanies some of the notes by jerks of the body backward and forward.

The song of *N. fasciatus* could be confused only with *N. bruneri* and *Anaxipha exigua*. The former is generally weaker and with a much more rapid tremolo, which is clearly evident only at rather low temperatures. The latter is similar in movement but much more musical and bell-like in quality than any *Nemobius*.

The song of *N. fasciatus tinullus* differs from typical *fasciatus* only in the frequency of chirps. Instead of appearing like a continuous sound the separate chirps are evident at all temperatures. By estimating the rate as previously described, when too fast to count, specimens at Mt. Pleasant, Iowa were found to chirp at the following rates per second: 7 and 8 at 80° F., 5 and 5.7 at 66°, 4.4 at 65°, 4.3 and 5 at 61°, and 3.8 at 59°. Specimens from Raleigh, North Carolina gave the following rates: 7 at 82° F., 8 at 79°, 7 at 75°, 6 at 69°, 5.5 at 67°, 5 at 66°, 4 at 60°; from N. C. mountains: 7 to 8 at 80°, 5 at 66°. In the mating song the notes sounded at about half the above rate, less rhythmically but sharper and more emphatically.

The song of *N. fasciatus socius* differs from the other two races in tone quality and in the method of production. In place of brief sharp chirps, the notes are longer and appear to be a combination of a low buzzing sound and a weak shrill sound. When the movement of the tegmina is observed at ordinary summer temperatures it appears to be a single slow inward movement for each note. When observed at lower temperatures it becomes apparent that each movement is accompanied by a rapid vibration of the tegmina, with a short amplitude. With the temperature near 60° F., there is a perceptible quaver in the notes, which are longer and slower than at higher temperatures. In cool weather the notes seem to be clearer and the shrill quality is more evident. It seems probable that vibrations caused by the teeth in the file produce the shrill element in the sound and that at high temperatures this passes beyond the range of human hearing leaving the buzzing sound caused by the tegminal vibrations as the most audible element of the sound.

Males of *socius* show considerable variation as to the frequency of notes and the same individual may vary the rate from time to time. Rates per second observed at different localities are as follows: Ames, Iowa, 2.5 to 3 at 77° F., 4 at 80°; Raleigh, N. C., 3 to 5 at 86°, 4 to 6 at 88°, Ripley, W. Va., 3 at temperature probably over 90°; Geneva, N. Y., 3 to 5, crickets in the sunlight and temperature well above 80° in the shade. At 66° a Raleigh male sang only 7 notes in 5 seconds.

The presence of a female influences the rate of notes even when the male is not singing his characteristic mating song. Three Raleigh males caged alone had somewhat different usual rates. At 86° F. they ran about 3, 4 and 5 notes per second respectively. When females were placed in the cages it was noticeable that after a few minutes all three were singing faster. The third increased to about 7 per second, the second to nearly 8 and the first only to 4 or 5. The mating song is similar to the above except that there is a brief pause after a series of 5 to 9 notes and the last note of each series is slightly prolonged with a decrescendo movement. This note is accompanied by a backward jerk of the body.

In a cage containing a large number of *N. socius* a slightly different note is frequently heard, especially among new arrivals from the field. As they meet when crawling about the cage

they will stop and sound one or two loud notes of about a second duration. It seems to result more often from the meeting of two males.

The song of *N. sparsalsus* has almost no rhythm. Notes of a half to one second duration may be repeated for a time with some regularity at a rate of about 3 in 5 seconds but, at intervals, longer and louder notes of 2 or 3 seconds duration are thrown in. The song is not loud considering the size of the cricket and the quality is like a shrill sound and buzz combined. Individual notes, especially the longer ones, remind one of *N. cubensis* in that they increase in volume and pitch. The mating song is brief chirps at the rate of 3 or 4 per second. These generally come in series of 2, 3, or 4 with slightly longer pauses between. Longer notes are frequently mixed in with the short chirps.

The song of *N. maculatus* is comparatively weak. It is a continuous buzzing trill with a constant rhythmical undulation in volume having a frequency about equal to the chirping rate of *tinnulus*. On cool days a very rapid tremolo is apparently corresponding in time to the strokes of the tegmina. The undulations or beats each cover a number of strokes. An Iowa specimen at 61° F. had thirty-six beats in ten seconds; at 70° about six per second. No distinct mating song has been observed.

The song of *N. griseus funeralis* is the most monotonous of any of the genus. It is a low weak buzz with a faint shrill overtone. It can be identified by the frequent breaks or pauses of a small fraction of a second that come at intervals of 5 to 10 seconds with little regularity. At times it may continue for 15 to 30 seconds without a break. As the sound is resumed after each break it starts with reduced volume and pitch in a crescendo movement covering a third to half a second after which a uniform tone is maintained. The mating song is very brief sharp chirps of possibly a fifth of second duration, produced without regular rhythm at an average rate of 14 in 10 seconds at 78° F. During this song the male jerks its body forward and backward.

The song of *N. bruneri* somewhat resembles that of *N. maculatus* in its extremely rapid tremolo but lacks the beats. It is as if the song of typical *fasciatus* were speeded up to such a high frequency that the tegminal strokes are barely perceptible.

It is a continuous trill like that of *Oecanthus nigricornis* but weaker and higher pitched. The pitch must be close to the upper limit audible to the human ear. Only one type of song is produced.

The writer heard *N. mormonius* singing along the edge of a small stream on the Bright Angel trail in the Grand Canyon, and described it in his notes as a continuous trill resembling the song of *Oecanthus nigricornis*. At that time he did not know the songs of the other species and could not make critical comparisons.

The songs of *N. cubensis* and *N. palustris* are very much alike. Both have notes of several seconds duration with approximately equal intervals of rest. The pitch is very high and the quality may be described as a thin whistle, meaning that the sound is not a pure musical tone. The song of *palustris* seems to be a little clearer than that of *cubensis*. Each note very gradually increases in volume until it ends abruptly. At Geneva, N. Y. on a hot day the notes of *palustris* were observed to be 5 to 10 seconds in length and the rests 5 to 10 seconds. At Raleigh, N. C. no difference in the song could be noticed. The species here has paler colored legs, head, and pronotum and is close to if not identical with *N. palustris aurantius* Rehn and Hebard.

The song of *N. cubensis* observed at Raleigh, N. C. had notes and rests usually from 8 to 15 seconds in length but some notes were as short as 2 seconds and others as long as 30 seconds. As a rule each male, when singing regularly has a fairly constant length of note. One at Carolina Beach had notes regularly 10 seconds long. No special mating song has been observed for either of the above species.

The song of *N. ambitiosus* was determined from living specimens collected in Dixie Co. and Alachua Co., Florida, by T. H. Hubbel. It has a rather low pitched song compared to some of the other species and the quality is rather musical and pleasant. When the crickets arrived, April 2, it is probable that none had been in the adult stage very long judging by the fact that many were still nymphs. For a while they all sang at a rather slow rate of about 6 notes per 10 seconds. Each note has a slight crescendo movement and ends abruptly. There is also a noticeable tremolo effect. A week after they arrived one was observed to have speeded up the song and was found to be

singing to a female. The rate was very changeable from 10 to 20 notes per 10 seconds at a temperature of 77° F. Sometimes the notes were very brief and weak, about one per second, at other times they were drawn out to nearly two seconds each with very brief pauses between so that the song was almost continuous. On another day, at 77° F., one was singing 15 to 16 notes in 10 seconds and another 9 to 12. At 61° F. one sang 5 notes in 10 seconds and another at 58° 6 notes in 10 seconds. At these temperatures the notes were very weak and distinctly tremolo. Only one male from Dixie Co. lived and it never sang at as fast a rate as the others. At 87° it had 8 notes per 10 seconds and at 80° only 7 notes.

The song of *N. carolinus* reminds one of the distant droning of some species of cicadas. The tone quality is like that of *N. griseus funeralis* and *N. confusus*, a low buzz with a thin shrill overtone. At times it has a rhythmical beat like the song of *maculatus* but a little more rapid. It sounds as if the singer were quivering with nervous energy. If one listens to a single song closely, the beat will be found to die out and the song will run along at reduced volume, sometimes seeming about to die out. Then it will gain in force again and tremble as before. Rarely males will be heard that seldom sing without beats but usually there is a regular repetition of the two phases of the song, sometimes one second for each period and sometimes longer. Sometimes when starting to sing this species will sound a few notes which increase in volume and then die out. No special mating song has been observed, although the song as described above has been heard many times both in Iowa and North Carolina and the two sexes have been caged together.

The most unique song in the genus is that of *N. confusus*. It has a constant meter of two brief weak notes and a longer louder one. Some individuals have been heard with three of the weak notes. The weak notes can be heard only a few feet away so that at a little distance the song seems to be a repetition of a single note, the loud one. The three notes are really not distinct but are a single note with two short rises in volume and then a greater increase till the end of the note after which there is a brief pause before the next is started. It is a droning buzzing trill like the song of *carolinus*. The rate of song varies somewhat. One in Iowa, at 70° F., was observed to

start at a rate of one complete note per second and at times increased to two per second. At Raleigh, N. C. one sang with 9 to 10 notes in 10 seconds at 75° and 10 to 12 notes at 80°. No special mating song has been observed, although males have been caged with females.

MATING HABITS.

Preliminary to mating the male faces the female and sings. In many species it has a special mating song for such occasions. At the same time it performs something like a dance by jerking

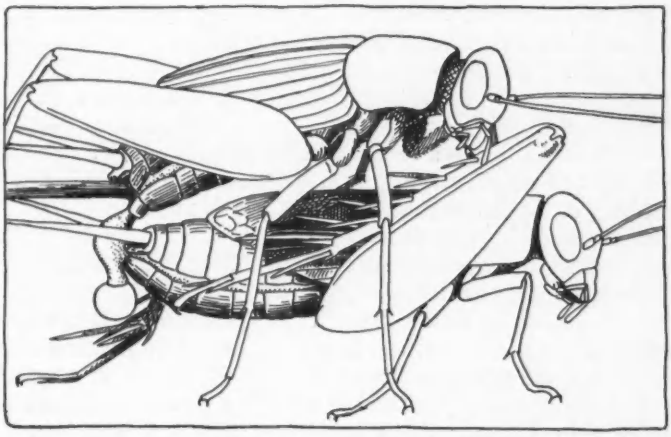


FIG. 4. Female (upper) feeding on secretion of specialized spine on male hind tibia during mating.

the body backward and forward without changing the position of the feet. The genitalia are protruded as shown in Fig. 5, D, but the spermatophore is not formed until a short time before mating takes place. It appears in a partially formed condition as a slightly elongated drop of milky white viscous liquid which is pushed out of the genital opening. It soon becomes spherical and remains suspended from the concavity formed by the extremity of the fleshy ventral portion of the genitalia.

Shortly after this the male turns around, drops the tegmina and backs toward the female. At the same time it raises one hind femur with the tibia closed upon it and brings it forward so far that it is inverted. The female crawls over the male

and begins to bite at the specialized proximal internal spine on the hind tibia. This brings the female far enough forward that the male can push the claspers into the opening between the ovipositor and subgenital plate (Fig. 4). They remain in this position usually from 15 to 25 minutes, the female all the time biting at the spine, sometimes running the mouth along the tibia but always coming back to the proximal internal spine. When she leaves the male, the spermatophore remains attached to her and later she removes it and eats it.

The specialized structure of the proximal internal spine of the male hind tibia, has been published on by Pantel (5) but he did not know its function. It stands perpendicular to the tibia and is much thicker and shorter than the same spine in the female. The base is dark while the apical portion is white and thin walled. In some specimens it has a dark slightly hooked tip, but in the majority, the apical portion has been removed probably by a female cricket (Fig. 5, A, B). Parts of some of the neighboring spines are sometimes missing also. Speaking of the internal structure of the modified spine Pantel says that the "hypoderm forms a massive tissue, a sort of muff of thick wall with cavity very much reduced." The constitution of the contents of the cavity he says is "undecipherable in my preparation." What he found in the cavity was probably a viscous secretion. If a male cricket is etherized and one of the mutilated modified spines is touched with the point of a pin, a viscous liquid usually adheres to the point and will pull out into a thin thread. After repeating this a few times, the supply seems to become exhausted.

There can be little doubt but that the function of the modified spine is that of an alluring gland similar to the metanotal gland in *Oecanthus*. Females have sometimes been observed to bite at the spine when no mating is taking place, but the male does not permit the female to continue this unless a spermatophore is being formed.

The fully formed spermatophore (Fig. 5, G) has a spherical body about one and a third millimeters in diameter and with a flattened curved tube about two and a half millimeters long. Near the tip there is an expanded portion, molded in the groove between the claspers. The extreme tip curves slightly in the opposite direction. The walls and tube are composed of a clear hard substance. A capillary opening extends through the tube to the tip.

The formation of the spermatophore is a complicated process which is difficult to understand. When it first appears on the male it is sometimes possible to etherize the cricket without dislodging the spermatophore. If it is examined in place, we find the forming tube as a narrow ribbon of viscous liquid extending along the groove between the inflated lips on

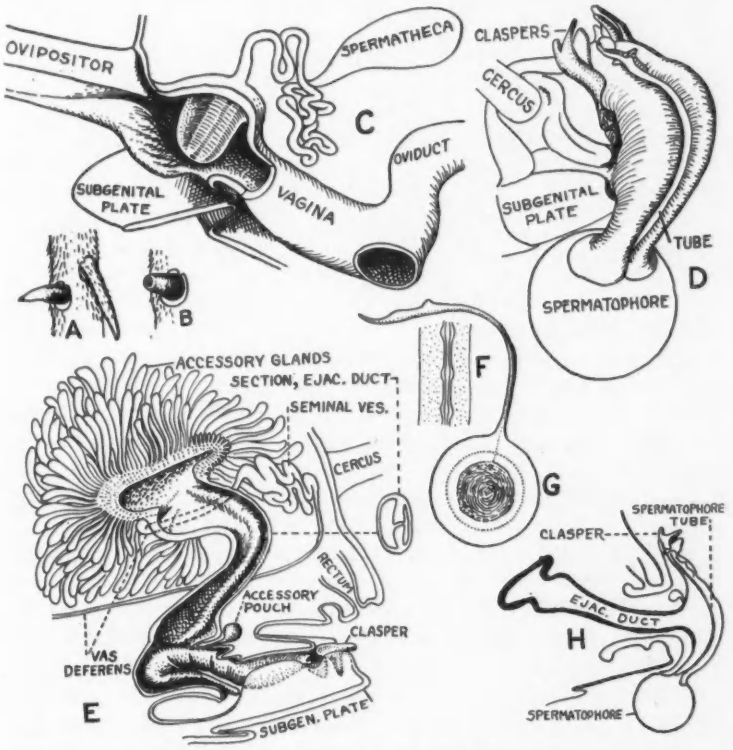


FIG. 5. A, Specialized spine of male hind tibia (left) and unspecialized spine (right). B, Specialized spine as usually found with tip removed. C, Female genital organs, showing knob-like invagination of dorsal wall of vagina. D, Male external genitalia during formation of spermatophore, caudo-lateral view. E, Male genital organs in resting position, as if cut through the median line. F, Portion of spermatophore tube in semi-liquid condition showing included capillary tube of different substance. G, Spermatophore, showing central sperm mass (shaded), surrounding liquid and hardened outer wall. H, Diagram of approximate position of male organs during spermatophore formation.

the caudal aspect of the genitalia, from the body of the spermatophore to the distal end of the rigid groove between the claspers (Fig. 5, D, H). If this strip is examined under a microscope while still in a semiliquid condition there appears to be within it a thin walled capillary tube of different substance, which is easily broken by handling as if it were also in a semiliquid condition (Fig. 5, F). This tube extends into the body of the spermatophore.

If the body of the spermatophore is compressed under a cover glass while still a milky liquid, the sperm mass is found to be already present. The surrounding substance becomes clear in a few minutes and under the microscope becomes granular in appearance. Thin streams of liquid carrying granules are seen moving away from the edge. The substance appears to be a colloidal solution in which a clotting action is taking place, with a squeezing out of a liquid phase toward the center.

The normal development of the spermatophore can be followed best by suspending it under a cover glass without crushing it. As soon as it clears the sperm mass can be seen surrounded by a thin membrane. For several minutes the sperms can be seen swimming around in the mass all going in the same direction. The outer surface of the spermatophore, which is like a thin membrane at first gradually becomes thicker and harder. The sperm mass is surrounded by a layer of liquid. By contraction of the outer wall a pressure is developed which breaks the thin side where it is flattened by the cover glass and the sperms pour out. The thin membrane surrounding them collapses and empties. The central cavity is then filled with a liquid in which some further clotting takes place, forming suspended particles and fern-shaped concretions.

When the spermatophore has been allowed to harden normally on the male the pressure developed by hardening and drying will force the sperms through the capillary tube. If this inner tube becomes dislocated, as usually happens when the spermatophore is removed before completely formed, the contraction of the outer wall results in a gaping split, releasing the contents. If immersed in water, the outer wall takes up water, expands, and the split closes again.

While the spermatophore remains attached to the female, the sperms pass into the seminal receptacle or spermatheca. The tip of the spermatophore tube must enter a small hole in a

knob-like invagination of the dorsal wall of the vagina, situated above the base of the subgenital plate between a pair of fleshy pads attached to the ventral rods of the ovipositor (Fig. 5, C). This knob has a thin but somewhat rigid wall and is about the right size to be grapsed by the male claspers, which would bring the tip of the spermatophore tube close to the hole in the apex of the knob. A tube passes through the knob, and with many convolutions leads to the spermatheca.

The complicated male organs are shown as if cut directly through the median line in Fig. 5, E. There are a large number of accessory glands which undoubtedly secrete the substance of the spermatophore wall. A dorsal group of these are very small, short tubes. The large common duct has lateral invaginations which meet and divide the space into two passage ways. Near the base of the claspers there is a pair of thin walled pouches of unknown function. The ventral thin walled portion of the external genitalia is much inflated in use and is folded up when withdrawn into the body.

ECOLOGY.

As previously pointed out the recognition of the characteristic type of song for each species of *Nemobius* has greatly simplified the study of their distribution. I would frequently check up on my memory by capturing a specimen if there was any doubt about the identity of the song. Once the songs have been thoroughly learned, it is only necessary to listen carefully to determine what species are present and their approximate abundance in any locality.

There is a surprising exactness about their distribution. Once the rules have been learned one can look at a varied landscape and enumerate what species of *Nemobius* will be found in the various parts of it. Some species range widely and others are narrowly restricted in their environment. Unlike many insects these crickets are not bound by specific plant food relations, but their occurrence is rather closely related to the plant community. Without experimental verification the following factors seem to influence the choice of habitat: moisture, ground cover, food supply near the ground level, temperature or sunlight and shade relations. If a combination of factors favorable to any one species is generally found in a plant community, the local distribution of the cricket will follow that community.

The species which are commonly associated with certain plant communities in North Carolina are given below, taking up first the successional stages originating from an abandoned field, as outlined by Wells (6).

1. Crab grass (*Syntherisma sanguinale*) *Nemobius fasciatus socius*. This passes into an association of tall weeds with consequent elimination of grass, becoming an unfavorable habitat for *socius* when complete.

2. Broom-sedge (*Andropogon virginicus*) *Nembius griseus funeralis*. This stage follows the tall weeds. Some *socius* may be found in it, but *funeralis* is often the only species especially on sterile soils where the clumps of *Andropogon* are well separated.

3. Pine woodland, (*Pinus taeda, P. echinata*) *Nemobius fasciatus tinnulus*. In the intermediate stage, before the pines have crowded out the *Andropogon*, *N. funeralis* may still be found between the pines. As soon as the pines attain size enough to cast considerable shade, *tinnulus* comes in.

4. Oak woodland (*Quercus marylandica, Q. stellata*) *Nemobius fasciatus tinnulus* and *N. confusus*. The latter, which is never abundant, can tolerate deeper shade than the former.

5. Mesic forest (*Quercus, Carya, Acer, Fagus*) *Nemobius maculatus, N. confusus, N. Carolinus*. The last may be found in locally moist places in any of the successional stages leading up to the climax, but becomes more numerous and widely distributed in the climax forest.

6. Salt marsh (*Juncus roemerianus, Spartina stricta*) *Nemobius sparsalsus* and *N. cubensis*.

7. Fresh water marsh (*Typha latifolia, Scirpus* spp.) *Nemobius cubensis, N. carolinus, N. fasciatus socius*. The last is not found under tall marsh plants.

8. Swamp forest (*Nyssa aquatica, Taxodium distichum*) *Nemobius carolinus*.

In the northern states *N. fasciatus fasciatus* is the most common species. It is found in all grass land except very wet marshy places where *socius* is found. This relation has been observed in New York and W. Virginia, Iowa, Colo., and the mountain sections of Virginia, and North Carolina. In Iowa where its distribution was studied more thoroughly, it attains greatest abundance in the blue grass (*Poa pratensis*) pastures, which are commonly found in small valleys. On the borders of marshes and near small sluggish streams it sometimes occurs with *socius* but does not extend into the wet undrained ground.

Near Raleigh, N. C. it was found during October and November 1930 in a few small areas on fertile flood plains along the Neuse River. These places were partially shaded and had a greater development of mesic grasses than is com-

monly found in the Piedmont. The dominant grass species were *Agrostis perennans*, *Muhlenbergia sylvatica* and *Poa pratensis*, all northern grasses approaching their southern limits here. In one large pasture on the river flood plain, *fasciatus* was found around the borders where there were trees and a few could be found near single trees in the open, but the rest of the area was inhabited by *socius*.. In another place it was abundant among the above mentioned grasses on a high bank over the stream, where there were scattered trees and *Crataegus* bushes. In this small narrow strip there were almost no *socius* present but a hundred feet back from the stream in treeless portions of the field *socius* was common and *fasciatus* rare.

The most important environmental factors for *fasciatus* seems to be a good growth of grass without excessive moisture. It is tolerant to a degree of shade that does not interfere with the growth of grass and in the south may even demand shade.

N. socius, as recognized in this paper, is associated in the northern states with poorly drained grass land such as low prairies, pond and marsh borders, and low moist meadows and pastures. Restricted to such situations it has been observed in New York, Ohio, West Virginia, Iowa, Colorado, New Mexico, and in the mountains of Virginia and North Carolina. It was the only race found in the moist meadow along the stream at Pingree Park, Colo. at an altitude of over 9000 feet. In Iowa it could be found along small sluggish streams, often with *fasciatus*, and a few scattered individuals were observed in well watered lawns where *fasciatus* was dominant. It was found most abundant in a low undrained prairie bordering a marsh but not in the central area under the taller marsh plants.

In the Piedmont and Costal Plain of North Carolina *socius* is more abundant and more widely distributed. It occurs in all short grasses and clovers such as those found in lawns, pastures and abandoned fields. In very sterile soils where grass grows sparingly, it is rarely found and *funeralis* takes its place. For some reason it can tolerate a much dryer habitat in the south, but as in the north it attains greatest abundance in low moist meadows and borders of marshes.

In the Piedmont and Coastal Plain of North Carolina *N. fasciatus tinnulus* is found in nearly all oak and pine woods except on the xeric sand ridges where no species of *Nemobius* has been found. It becomes most abundant in the more open

woods where some grass is growing. In the mountains the mesic forest type prevalent there is not favorable for it, and it becomes largely a forest border species. At Mt. Pleasant in southeastern Iowa it occurred where the woods were open enough to permit grass to grow. To sum up, the favorable factors for this race seem to be moderate moisture, a ground cover of dead leaves, the presence of grass or other low food plants, and possibly shade.

N. sparsalsus has only been found in salt marshes. When first found it was abundant out in the *Spartina* zone at the edge of the sound at low tide. At another time, during a high tide when the marsh was almost entirely flooded it was even more abundant among *Juncus* at the water's edge, apparently having been driven back by the water. No explanation can be offered for the restricted habitat of the species.

N. maculatus is strictly a forest species. Near Raleigh, N. C. it has been found only in the mesic type of forest which occurs there mostly along streams. It lives among the dead leaf ground cover on flood plains and hills but not in sloughs. In Iowa it seems to be somewhat more abundant along the edge of woods where there is grass as well as leaves on the ground, but occurs also in dense forest both on hills and flood plains. The species seems to be tolerant to a moderate range of moisture conditions but demands dead leaf cover or shade or both.

Specimens of *N. griseus griseus* were collected for the writer by E. M. Walker who writes that the species is extremely local in Ontario and that "it seems to prefer dry sandy pastures, covered with short grass, sedges (2 or 3 inches high), *Antennaria*, and the low-growing mosses of such situations." In this choice of a xeric habitat it is not unlike its southern relative.

N. griseus funeralis can tolerate more xeric conditions than any other species found in North Carolina. It has been found most commonly associated with broom-sedge (*Andropogon*) but not in very dense stands for this grass apparently serves as shelter rather than as a food plant. Where small grasses such as *Aristida oligantha* or small clovers like *Lespedeza* grow between clumps of *Andropogon*, it is found in greatest numbers but never becomes very abundant. A few have been found in crab grass (*Syntherisma*). It is very secretive in habits and seldom comes out from under the plants and for this reason has been a rare species in collections.

N. bruneri is a stream border species both in North Carolina and in Iowa. It is not found on small deeply shaded streams for it seems to demand at least a small amount of sunlight. It is most readily found on gravel bars, in company with *Paratettix* and Gelastocoridæ. When disturbed it quickly jumps from the shelter of one rock to another. It has also been found on sandy banks where some grass or accumulated dead leaves furnish a shelter.

The near relative of the last species, *N. mormonius* is also found along streams, but in the arid west where it occurs such places are about the only situations where a species of *Nemobius* could be expected to exist.

N. cubensis is largely a marsh species, living both in fresh water marshes and in the *Juncus* zone of salt marshes. It is not confined to excessively wet places for it can also be found along stream banks and in other moist situations where it is protected by a thick covering of honeysuckle, high grass, or bushes. It has never been found by the writer on *Sphagnum* in company with the closely related *palustris*. Where patches of the moss grow along side of tall grasses *palustris* will be found in the former and *cubensis* in the latter.

N. palustris seems to be strictly an associate of *Sphagnum* and is found no where else. It can live in a jar and develop from the nymph to adult with no other food than *Sphagnum*. The eggs are deposited in the moss when they have a choice between that and soil.

The writer has not observed *N. ambitiosus* in the field for it has not been found in North Carolina. Two lots of living specimens sent by T. H. Hubbel were accompanied by notes on their habitats. The habitat of the first lot from Dixie, Co. Fla., was described as "open sunny grove of *Quercus catesbaei* on whitish sandy soil, little undergrowth, much bare sand exposed, xerophytic habitat." The second habitat at the University of Florida Biological Station, Newman's Lake, Alachua Co., Fla., was described as "magnolia-oak-hickory-sweet gum hammock on sandy ridge, mesophytic habitat, forest floor covered with dead leaves and herbage, several inches of leaf mold over sandy loam." Hubbel also called attention to the fact that nymphs from the first habitat were grayish in color while those from the second were darker and more brownish in color. The most striking difference was in the color of the abdomen. Those from the sand ridge had a grayish white

ground color with several rows of paired, black spots in the median portion except the fourth segment which was entirely black. In the other lot the median area was sepia with only one paired row of black spots at the margins of the area. The remainder of dorsal area was of paler ground color with three paired rows of spots. The fourth segment was only slightly darker than the others. No striking difference was discovered between the adults of the two lots.

The nymphs of a second generation reared in the laboratory at Raleigh under identical conditions showed the same striking difference in color. This would indicate that there is some inherent difference between the crickets from the xeric habitat and those from the mesic environment. Further study might show that we have in this species another example of physiological differentiation taking place.

The most widely distributed species from the standpoint of plant associates is *N. carolinus*. The most important factor controlling its distribution seems to be moisture. Locally moist spots in an otherwise xeric habitat may have a colony of these crickets. It is an inhabitant of gullies, and seepage spots, in any plant community. With ordinary soil moisture it lives only under the protection of a dense cover of honeysuckle, thick bushes or matted grass. It is found most abundant in marshes and wooded ravines and sloughs. In swamp forest it is the only species found and in *Sphagnum* it is the only associate of *palustris*. In woods in southeastern Iowa it was abundant on level spots near the streams but on the slopes was replaced by *confusus*. Along open stream borders it is associated with *bruneri*.

N. confusus is another species confined to woods but it prefers the well drained slopes and uplands. It is never very abundant but is most often found in deciduous forest where it lives in the dead leaf ground cover. A few have been found in pine woodland, hiding under the bed of needles. Near Raleigh a large number were found in a patch of partridge berry (*Mitchella repens*) growing in an oak woods. Unlike *tinnulus* it is not partial to the more open grassy places and does not demand the more mesic forest type as in the case of *maculatus*. In southeastern Iowa it was found in oak forest, climax forest and sparingly near forest borders and under shrubby growths, always among dead leaves.

SUMMARY.

The discovery of specific characters in the male genitalia makes it possible to identify the males of the genus as readily as the females. Evidence furnished by such characters changes the status of *N. mormonius* Scudder from that of a subspecies of *N. cubensis* Saussure to a distinct species with closest relationship to *N. bruneri* Hebard.

N. fasciatus tinnulus new subspecies, is described and the conception of the status of *N. fasciatus fasciatus* (De Geer) and *N. fasciatus socius* Scudder is changed from that of a geographic one based on the relative length of the ovipositor, to a new conception of the above three subspecies based on certain characters in both sexes and which is correlated with physiological differences manifested in ecological distribution, seasonal history and song habits.

The song habits of the most of the species and subspecies found in the United States are described. Many species have a special song heard only when they are mating.

It has been found that the macropterous forms may remove their wings voluntarily.

The specialized proximal internal spine of the male hind tibia functions as an alluring gland. The formation of the spermatophore and the genital anatomy of both sexes is described.

In their ecological distribution the species of *Nemobius* are not bound by specific plant food relations, but are influenced by other factors which may confine them to certain plant communities. The observed environmental relations of all the species studied are described.

LITERATURE CITED.

(1) **Hebard, M.** A Revision of the Genus Nemobius found in North America north of the Isthmus of Panama. Proc. Acad. Nat. Sci. Philadelphia, 1913, pp. 394–492.

(2) **Fulton, B. B.** Physiological Variation in the Snowy Tree Cricket. Ann. Ent. Soc. Amer. 18: 363–383, 1925.

(3) **Allard, H. A.** Variation in the Stridulations of Orthoptera. Ent. News, 23: 460–462, 1912.

(4) **Blatchley, W. S.** Orthoptera of Northeastern America, pp. 1–784, Indianapolis, Ind., 1920.

(5) **Pantel, J.** Notes Orthopterologiques IV, Sur quelques particularites de l'armure des pattes en sur l'avortement des ailes dans le genre Nemobius. Anal. Soc. Espan. Nat. 25: 47–58, 1896.

(6) **Wells, B. W.** Major Plant Communities of North Carolina. N. C. Agr. Exp. Sta. Tech. Bul. 25: 1–20, 1924.

THE RELATION OF TEMPERATURE AND RAINFALL TO OUTBREAKS OF THE GRAPE LEAFHOPPER, ERYTHRONEURA COMES SAY

JOHN R. EYER,
State College, New Mexico.

While conducting investigations on the life history and control of the grape leafhopper (*Erythroneura comes* Say) in Erie County, Pennsylvania, the author had occasion to observe a series of outbreaks of this insect and to accumulate certain pertinent bits of information concerning the relation of weather factors to such outbreaks.

The particular series of outbreaks under observation occurred from 1920 to 1925 and were characterized by the leafhopper becoming increasingly abundant during the years 1920 to 1923, the outbreak reaching its climax in 1923, and the insect then decreasing in abundance in 1924 and 1925 so that it was not an economic factor during these two years. At this time, in collaboration with the Department of Entomological Extension of the Pennsylvania State College,* yearly surveys were made of the leafhopper population in representative vineyards in Erie County for the purpose of forecasting spraying data and for keeping records of the seasonal history of the insect in relation to weather fluctuations. These resulted in the assembling of detailed and accurate records of the activities of the insect in relation to the weather conditions obtaining for the period of years mentioned, and an attempt has been made in the following discussion to determine by the customary methods of statistical correlation the probable relation between these weather factors and the fluctuation in leafhopper abundance.

Since the relation of weather factors to insect outbreaks is hard to elucidate, owing to the difficulty in disentangling the

*The author wishes to acknowledge his indebtedness to Dr. D. L. Van Dine and Professor H. N. Worthley, of the Pennsylvania State College, and to Dr. T. L. Guyton, of the Pennsylvania Department of Agriculture, for assistance in the collecting of information relative to the habits and occurrence of the grape leafhopper in Pennsylvania and for the loan of their notes and data pertaining to this subject.

effect of abnormal weather not only on the insect itself, but also on its respective mortality factors (parasites, predators, disease, etc.), the author has followed as closely as possible the suggestions of Cook (1), 1927, regarding the collecting and analyzing of weather data in connection with insect outbreaks.

The question of parasitism and similar restraining factors may be dismissed by mentioning that during the four years of our observations in Erie County no insect parasites of the grape leafhopper were in evidence, nor were any permanent predators observed feeding on the leafhoppers during their breeding season. Johnson (2), in his studies in the Lake Erie region records one species of Hymenopterous parasite, *Aphelopis* sp. and two predacious enemies, (*Anystis agilis* Banks and *Diaphnidia hamata* Van D.), but does not find any of them sufficiently abundant to be considered as control factors. Moreover, no fungus diseases were observed in sufficient abundance to be considered as restraining influences. Consequently weather conditions were assumed to be the foremost apparent factors active in determining leafhopper abundance during the period investigated and the data bearing on these factors was collected and analyzed as follows:

1. First a survey was made of the literature on leafhopper outbreaks in the Lake Erie region to ascertain the exact dates of such outbreaks and to obtain expressions of opinion from the various recorders concerning the possible causes of such outbreaks.

2. This particular investigation was confined to that section of the Grape Belt known as the "Lake Erie region" so that the data compared included only outbreaks of close geographic proximity and, as nearly as possible, the uniform weather conditions offered by a homogeneous geographical area. The Lake Erie region is regarded as that portion of New York, Pennsylvania, Ohio, Michigan and Canada bordering on Lake Erie, and the Chautauqua Lake region of New York.

3. All available meteorological data was secured from weather stations in close proximity to the outbreak centers for all years covered by and immediately preceding and following the outbreaks.

4. Composite climographs or hytherographs covering this data from said stations were constructed for the outbreak and "non-outbreak" years. These were compared with each other and with climographs representing normal years and an estimate formed of the relative importance of meteorological variations in the ecology of the grape leafhopper during normal, outbreak, and repression years.

5. The suspected meteorological factors were then directly correlated with figures representing the abundance of the species during the years in question and correlations were also made between the

deviations from normal of the weather factors and the leafhopper populations for the same periods.

6. The conditions found to pertain to the particular area and outbreak studied were then compared with the conditions of earlier outbreaks to determine if the abnormalities of the suspected meteorological factors occur at all times in correlation with outbreaks.

I. *A Survey of the Literature on Grape Leafhopper Outbreaks with Particular Reference to Those Occurring in the Lake Erie Region of the United States.*

Outbreaks of the Grape Leafhopper in the Lake Erie region have been recorded prior to 1900 by Fitch (3), 1861; Bethune (4), 1868; Saunders (5), 1871; Cook (6), 1874; Lintner (7), 1887–88; Lockhead (8), 1899 and 1900. None of these authors attempt to account for the reasons of these outbreaks. During the period 1899 to 1902 a series of definite outbreaks occurred in the Lake Erie region which were noted in 1902 by Felt (9). Hartzell (10) and Johnson (2) also note the occurrence of these outbreaks in their accounts of later outbreaks in 1910 and 1911. During the same period Fletcher (11) records an outbreak near St. Catherines, Canada.

Slingerland (12), 1904, makes one of the first contributions to our knowledge of the ecology of grape leafhopper outbreaks as follows:

"An outbreak of that common grape pest, the grape leafhopper, unprecedented in extent and destructiveness in the annals of New York has occurred in Chautauqua County during the past three years.

"Apparently the life pendulum of the grape leafhopper has begun its downward swing after an 'up' period of great destructiveness for two years, for last season they were not so numerous, although millions of them went into hibernation in the fall of 1902."

Gibson (13) notes its yearly abundance in Ontario in 1905 and 1906 and its continued abundance in the Chautauqua Belt is recorded by Symons (14) in the United States year books for 1906 and 1907. Its occurrence in the Canadian and United States portions of the Lake Erie grape belts is apparently not recorded in 1908 and 1909.

Gibson (15) in 1910 records its increasing abundance in the Ottawa region and Sill (16) notes that it was especially troublesome during the summer of 1910 in the North East district of Pennsylvania. In 1911 a serious outbreak is recorded for Pennsylvania by Johnson (17), and for New York by Hartzell (10).

In 1912, however, the leafhopper decreased greatly in abundance with regard to which Hartzell (18) comments as follows: "The winter of 1911–12 proved to be severe and hopes were entertained that this would cause a high mortality among the hibernating adults. However,

with the arrival of spring, the leafhoppers emerged from their winter quarters in great numbers and seriously injured the young foliage in many vineyards. . . . . Considering the summer as a whole, considerable injury was done to vineyards; yet the injury was less than was expected because of the cool weather during June, July, August, and September. The weather conditions during this period were unusual as will be noted from the accompanying record.* The temperature for June was 106 degrees below normal, a daily deficiency of three to five degrees; July was slightly below normal; August gave a deficiency of 125 degrees, a daily average of four degrees; September temperatures were 59 degrees above normal or a daily excess of 1.7 degrees. In the months when growth is most active—May to September—there was a deficiency of 148 degrees, one degree daily. The amount of precipitation for May, August, and September was above normal, while June and July were deficient in rainfall. From the middle of July until the end of September there was an excess of rainfall and cloudy weather combined with low temperatures. There were only four clear days between July 15 and 31, and August had only one clear day, the others being cloudy or partly cloudy. The percentage of sunshine during August was 42 to 43 per cent below normal, while the rainfall was four inches, or 1-10 inches above normal, 40 per cent more than in a normal year. September had eleven clear days, 53 per cent of sunshine, 8 per cent departure from normal, and an excess of 0.13 inch or 4 per cent above the average. These abnormal weather conditions were unfavorable to plant growth and appeared to be especially detrimental to the grape leafhopper, since it prevented a second summer brood and apparently interfered with the health of the nymphs as well as the adults."

Johnson's (19) observations in 1911 with reference to periodic outbreaks of the grape leafhopper are as follows: "Periodically, however, some as yet unknown conditions seem to favor its multiplication and it spreads over wide areas. . . . . Such conditions applied in the vineyards of Chautauqua County in the vicinity of Westfield, New York, during the seasons of 1901 and 1902, when many hundreds of acres of vineyards suffered greatly from the injury wrought by this pest. In 1903 the insect disappeared to a considerable extent and serious injury was again confined to limited areas until the season of 1910. The insect is now manifestly on the increase and during the past season (1910) spread through large blocks of vineyards. In fact, toward the latter part of the summer its presence in more or less destructive numbers was evident throughout the entire grape (Lake Erie) belt."

Johnson (2), in his bulletin on the life history of this insect also comments quite fully on the occurrence of leafhopper outbreaks in the Lake Erie Valley and he records, in much the same manner as Hartzell, the outbreaks of 1901 to 1904 and of 1910 to 1912. His explanation of the possible cause of the latter outbreak is as follows: "During 1911

*Monthly Met. Summary, 1912, U. S. Weather Bur., Buffalo, N. Y.

the injury wrought by the pest was greater than in preceding years, and the infestation was more widespread. The summer was unusually hot, and this resulted in the development of an almost full second brood which worked great injury to the vines late in the season. Immense numbers of adults went into hibernation, and large numbers of them emerged and made their appearance in the vineyards in the spring of 1912. Early in the season of 1912, on account of the presence of so many overwintering adults, there was every indication that the injury by this pest would be very great. There was an apparently normal development of the first brood of nymphs, and by the middle of the summer the injury in many vineyards was quite severe. Fortunately, however, the months of July and August were unseasonably cool. The low temperatures which prevailed during these two months so greatly retarded the development of the nymphs of the first brood that only a small percentage of the adults transforming from them deposited eggs for a second brood of nymphs. Hence there was not such a great increase in numbers of the insect during the latter end of the season of 1912 as there was at the end of the hot season of 1911."

From 1912 until 1920 the leafhoppers were apparently not seriously destructive in the Lake Erie grape belt. In 1916 Hartzell (20) writes as follows: "Only present in numbers sufficient to inflict damage over an extended area (in Chautauqua County) about once in eight or ten years. In other grape regions of the state they are more abundant each season, considerable injury occurring to the vineyards during shorter periods. It is necessary that such places (referring to hibernating quarters) be comparatively dry and free from inundation if the insects are to survive."

With regard to the particular outbreak to be analyzed in the latter part of this paper, DeLong (21), 1922, reports as follows: "The grape leafhopper has been a very serious pest in the Erie-Chautauqua grape area along the south-eastern shore of Lake Erie for many years. . . . During the seasons of 1920 and 1921 the hoppers have caused great damage to hundreds of acres of grapes in this section. . . . ." Van Dine (22), in 1923, adds: "The high leafhopper infestation throughout the vineyards in the Pennsylvania section of the grape belt this season (1922) emphasized the need of control measures for this insect. . . . . In the grape section under consideration there was an average infestation of 64.25 leafhopper nymphs per leaf in the maximum infested vines. . . . . ."

Ross (23) reports the abundant occurrence of this insect on the Canadian shore of Lake Erie during the same period and comments as follows on the possible influence of temperature and rainfall on yearly abundance.

"The adults went into hibernation in immense numbers and this spring they emerged in full force, the mild winter having had little if any effect in diminishing their numbers. By the time the grapes were in leaf, most of the graperies were literally alive with leafhoppers. During the period the overwintering adults were on the vines, there were several heavy washing rains. For example, on May 25th there

was a rainfall of 1.23 inches, on June 11th, 3.08 inches, and on June 17th, 1.38 inches. These rain storms reduced the number of adults to some extent (we found hoppers washed into the soil) but not to a sufficient extent to prevent a serious outbreak."

From this summary of the literature we may come to the following general conclusions:

1. Definite leafhopper outbreaks similar to the one observed by the author in 1920 to 1923 occurred in the Lake Erie Valley in 1901, 1902 and in 1911.
2. These outbreaks were invariably followed by periods of scarcity or low abundance.
3. Certain observers, particularly Hartzell, Ross and Johnson, have noted that low temperatures or excessive rainfall might have served as possible factors in reducing the infestation, following such outbreak periods.

Before proceeding to present the climatological data concerned with the particular outbreak under consideration, the author will briefly explain the general location and characteristics of the region referred to as the Lake Erie region.

II. *Definition and Climatological Characteristics of the Lake Erie Region.*

Erie County, Pennsylvania, where the author's studies were carried out, lies on the south-east shore of Lake Erie, about midway between Cleveland, Ohio, and Buffalo, New York. By the United States Weather Bureau it is classed as a part of the Lower Lake Region, which includes mainly that region west from Lake Ontario to Lake Michigan. The climate of Erie County is influenced largely by its proximity to Lake Erie because the lake lies directly in the path of the prevailing westerly winds. Consequently, the Chautauqua (N. Y.) and Erie County (Pa.) grape belts extending along the southern shore of Lake Erie for a distance of about 200 miles and inland from two to six miles have a mild climate due to the tempering influence of the Lake, which gives long mild autumns with unusually late fall frosts and winters which are less severe than elsewhere in the Lower Lake Region. Lake Ontario, to the north-east, also exerts a tempering influence, especially when cold waves, attended by rapidly falling temperatures, sweep down from Canada. During such times the difference

between the northern and southern shores of the Lake are sometimes as great as 20°.

The average temperature for Erie County is about 50°, with an average minimum of 39° and a maximum of 56°. The average annual precipitation is about 38 inches. During the summer months the average precipitation is somewhat greater than during the other seasons, but with this exception the distribution of precipitation is remarkably uniform.

III. *Seasonal History of the Grape Leafhopper with Relation to Normal Weather Variations.*

Before proceeding to analyze the effect of definite meteorological factors on the grape leafhopper it is necessary to briefly describe the normal occurrence of the various life stages of the insect with relation to the seasons of the year. This information was adequately obtained by Johnson (2) in his work in Erie County in 1911 and 1912 and is briefly summarized as follows:

"The grape leafhopper hibernates as an adult among accumulations of leaves and trash in vineyards, but mostly in adjoining woodlands, hedgerows and pastures. It becomes active during the first warm days of spring and commences feeding on the new growth of almost any of the plants with which it comes in contact. With the unfolding of the grape leaves there is a general migration of the insect to the vineyards. In normal seasons this takes place about the middle of May in the vineyards of the Lake Erie Valley. After feeding for a few days the leafhoppers mate and oviposition commences early in June. The average length of the egg stage is from eleven to fifteen days. The nymphs commence to appear on the under side of the leaves about the 20th of June, and by the end of the first week in July a large percentage of the first brood has hatched and is present in one of the several nymphal stages, of which there are five. The average length of the nymphal period is about twenty-eight days, but with many it varies from twenty to thirty-five days. A few newly transformed adults may be found in vineyards from about July 7th to July 12th.

"In normal seasons, however, the majority of the first-brood adults appear after the middle of July. Observations of the development of the insect indicate that if the nymphal period is lengthened by low temperatures during the month of July, the number of adults of the new brood that will mate and deposit eggs for a second brood is quite small; whereas, if high temperatures prevail during the early part of July, a large number of the nymphs are likely to develop rapidly and make their transformation about the middle of July. These early maturing adults mate and deposit eggs, and the resulting second brood of nymphs is quite large.

"By the early part of September most of the nymphs of both the first and second broods have transformed to adults, although a small number of nymphs may be found on the foliage until quite late in the fall. Toward the middle and latter part of September the adults commence to migrate from the vineyards and during warm, calm afternoons may be seen in swarms drifting through the air in an apparently aimless manner. They usually come to rest in adjoining woodlands or rough pasture lands. Here they remain more or less active during the warmer parts of the days of October, seeking the shelter of leaves and trash at night and during the cooler days, and becoming less active as the cold weather of winter approaches."

IV. *Seasonal Life History of the Grape Leafhopper with Particular Relation to Temperature and Rainfall During the Period 1920–1925.*

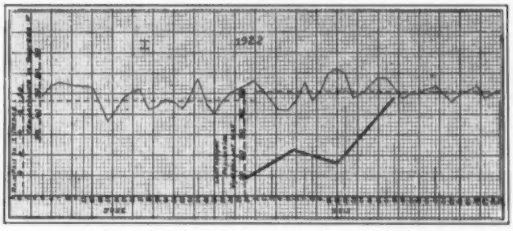
In comparing leafhopper abundance with weather conditions during this period the "leafhopper population" for each year is computed on the basis of the average number of nymphs per leaf from seven representative vineyards in Erie County. These vineyards were so located as to furnish this data from the western, central and eastern parts of the county and from the Lake-shore and inland grape growing areas. All weather data for Erie County was obtained from the United States Weather Bureau Station at Erie, this being a centrally located station with reference to the grape growing area of the county. The various comparisons made under this heading are discussed as follows:

1. Variations in abundance and periodicity of the leafhoppers with relation to the temperature and rainfall immediately attending their seasonal activities.
2. Relation of monthly temperatures and precipitations, particularly those of the spring and fall, to leafhopper abundance during outbreak and repression years as determined by hytherographs and mathematical correlations.

1. *Variations in Abundance and Periodicity of the Leafhoppers with Relation to the Temperature and Rainfall Immediately Attending Their Seasonal Activities.*

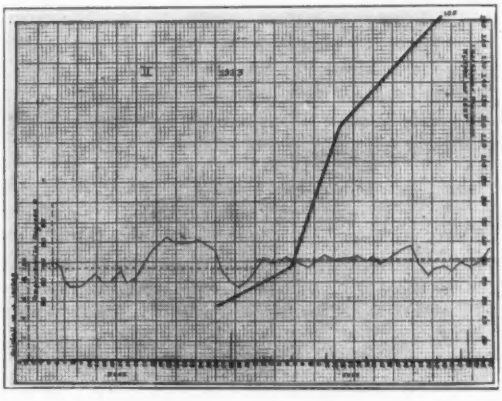
In Graphs I–IV, the yearly population counts for 1922, '23, '24, and '25 are compared directly with the daily mean temperature and precipitation records for the same periods, said periods commencing at the time the overwintering leafhopper adults commence laying eggs in the vineyards, which is approx-

imately June 1st for the Erie County region. Each population curve is constructed to cover the four points which indicate the dates on which the nymphs of the second, third, fourth, and fifth instars were found in maximum abundance rather than



GRAPH I. Relation of June and July Temperature and Precipitation to Leafhopper Population, 1922.

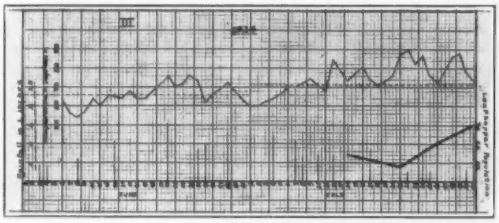
being based on counts made on the same dates of the series of years. In this way each point and intervening segment of the curve for a given year is directly comparable with the same



GRAPH II. Relation of June and July Temperature and Precipitation to Leafhopper Population, 1923.

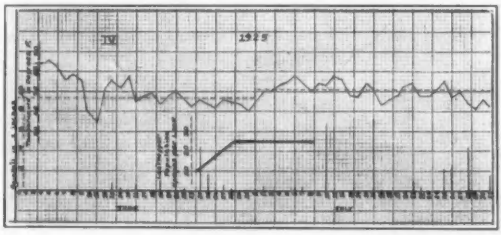
points and segments of the other curves of the series and the relative positions and inclinations of the comparable portions of each curve may be taken as indicative of the speed of development which took place during the particular season in question.

For example, in the curve for 1922, the second instar nymphs reached their maximum occurrences on June 30th, the third instar nymphs on July 6th, the fourth instar nymphs on July 11th, and the fifth instar nymphs on July 18th. In 1923 the



GRAPH III. Relation of June and July Temperature and Precipitation to Leafhopper Population, 1924.

dates for the maximum occurrence of the same series of instars were: second instar, June 26; third instar, July 6; fourth instar, July 12; and fifth instar, July 26. Comparing the increment in population in these two curves it can be seen that although



GRAPH IV. Relation of June and July Temperature and Precipitation to Leafhopper Population, 1925.

the transition from the second to the third instar was made in practically the same time interval and at approximately the same time of the year, the leafhopper population actually decreased during the interval between the third and fourth instars in 1922, while it increased greatly during the same period in 1923. Comparing the rainfall and temperature during the period immediately preceding the second instar counts (i. e., for the month of June) for the two years we see that the year

1922 was characterized by much more rainfall than was 1923 (i. e., the total June rainfall for 1922 being 2.1 inches and for 1923, 1.1 inches) while the comparative daily temperatures in excess of normal for the month of June for the two years are practically identical; i. e., 3.9° for 1922 and 3.8° for 1923. By applying this same method of analysis to the remaining portions of the curves for 1922 and 1923 and also to the curves for 1924 and 1925 we may conclude that in general the differences in leafhopper population between instars is more closely correlated with rainfall differences than temperature fluctuations and that in general dry years are accompanied by higher leafhopper populations than are wet years. This is remarkably well demonstrated in 1924, where the leafhopper population

TABLE I.

	1922	1923	1924	1925
1. First recorded appearance of overwintering adults in vineyards.....	June 2	May 31	June 9	May 29
2. Adults observed mating..	June 2–15	May 31–June 6	June 9–15	May 30–June 5
3. First instar nymphs recorded.....	June 15	June 12	July 8	June 10

either actually decreased or increased only slightly from July 14 to July 31 during a period of increasing temperatures accompanied by continuous and heavy rainfall.

In addition to offering variations in rate of increase in population and actual numbers of leafhoppers per season, these same curves show distinct differences with regard to the time of year when the leafhoppers make their appearance. In the two curves just compared (i. e., 1922 and 1923) the various instars from the second to the fifth reached their periods of maximum abundance at practically the same time of the year (i. e., second instar between June 26–30, third instar, July 6, etc.). This would allow us to assume that the overwintering adults appeared in the vineyards and commenced ovipositing at approximately the same time during the spring, 1922 and 1923. This is supported by our observations of adult activities during these two years which are tabulated in the first two columns of Table I.

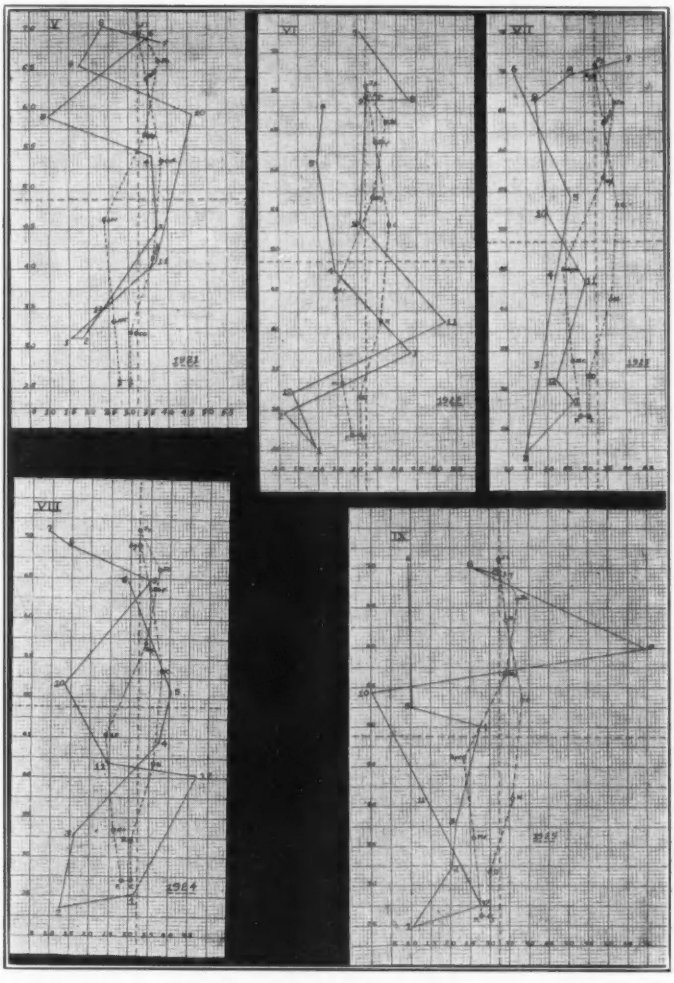
Comparing these data with those of 1924 and 1925, also included in the table, we see that these same phenomena were observed to occur somewhat later in these years, particularly in 1924, which were the years of greatest reduction in population. In 1924 the seasonal development of the leafhopper was so greatly delayed that most of the adults of the first generation did not develop until after August 10th, and the second generation failed entirely to develop. A similar situation during a year of repression has already been noted by Hartzell (18) in 1912. In 1924 the month of June showed a total precipitation of .8 below normal and in 1925 of 2.7 inches below. Hence, in these years, excess precipitation could not be regarded as a retarding factor with respect to time of appearance or rate of development. On the other hand, the average daily temperature deficiency for June, 1924, was 6.2°, thus furnishing a possible basis of explanation for the delay in development for that year. In 1925 the temperature for the month of June returned to more normal conditions, with an average daily excess of 4.8°, thus accounting for the almost complete return of the periodic events in the seasonal history of the leafhopper to their normal status.

Thus it appears that temperature may be a factor with regard to periodicity of occurrence, while rainfall influences the rate of increase and the establishment of a definite population. However, such an hypothesis, based on a cursory examination of comparative population, temperature, and rainfall curves must be more definitely established by the recognized methods of statistical analysis before it can be accepted. For this purpose we turn to an examination of the meteorological events of the entire year as expressed by climographs or hytherographs.

2. *Relation of Monthly Temperatures and Precipitations, Particularly Those of the Spring and Fall, to Leafhopper Abundance During Outbreak and Repression Years as Determined by Hytherographs and Mathematical Correlations.*

Graphs V–IX illustrate the yearly temperature and rainfall conditions pertaining in Erie County from 1921 to 1925, inclusive. The period 1921 to 1923 is characterized by increasing yearly populations and 1924 and 1925 by sudden and rapid declines. These diagrams are constructed so that the mean

temperature and total rainfall for each month of the year may be easily compared month by month. Also, to facilitate comparisons, each hytherograph is superimposed on one of lighter character (indicated in dotted lines) representing



GRAPHS V–IX. Temperature-rainfall Hytherographs for Leafhopper Outbreak Period, 1921–1923, compared with those for Repression Period, 1923–1925.

the normal temperature and rainfall records for each month of the year; and the yearly normals for both temperature and precipitation are indicated by heavy dotted lines crossing the hytherographs at right angles to each other.

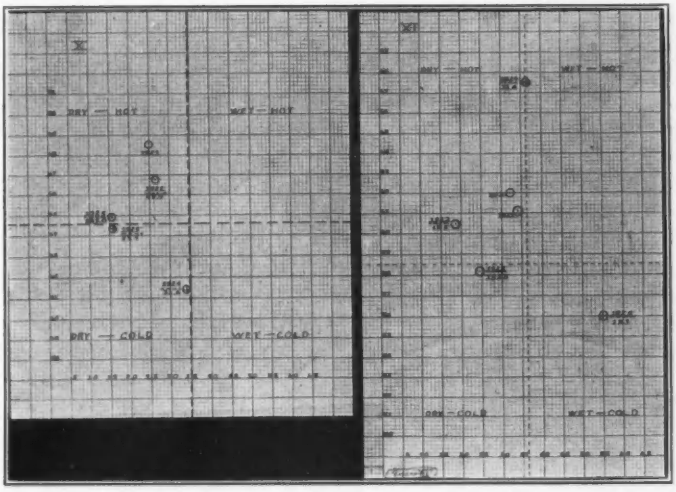
Owing to the fact that the period of most active increase in leafhopper population occurs usually in late June and July (see Graphs I–IV) the climographs are constructed to include one-half of each current year; i. e., the late summer, fall and early winter (July to December of the year preceding the outbreak or repression period to be analyzed), combined with the late winter, spring, and early summer (January to June) of the year under observation, dividing these two periods, however, between June and July rather than between March and April, because the developmental apex of the species occurs in July and is, as already shown in Graphs I-IV, activated to a large extent by the temperature and rainfall occurring in June and to a lesser extent by the same factors in the months immediately preceding June. Following the suggestion of Tehon (24), the ascending division of the hytherograph is called the "spring trend" and the descending division, the "fall trend." The two are separated in the diagram by omitting the connecting line between the point for July of one year and that for June of the following year.

These diagrams show that none of these years approaches the normal very closely, but when the spring and fall trends of each are compared respectively, certain similarities or differences are noted. For instance, in examining the spring trends of the years 1920 to 1925 we see that they become successively drier until 1924, during which year April and May show rainfall excesses of 1.3 and .65 inches respectively and, in addition, May and June evidence daily temperature deficiencies of 6.2° and 1.5° respectively. This, it will be recalled, is the first of the two years of reduced population. In 1925 spring conditions again return to the dry side of the hytherograph but the fall trend of the preceding year, 1924, evidences abnormalities both with respect to rainfall (i.e., July with an excess of .17 inches and September with 3.7 inches) and temperature (July with 1.9° daily deficiency and September with 3.4 daily deficiency). From this evidence we may roughly conclude that weather abnormalities, such as excessive moisture and low temperatures, during the breeding and ovipositing

period of the first generation in May and June or possibly of the second generation in July may exert a restraining influence. To a lesser extent perhaps would these same influences be a restraining factor in September when the insect commences its migration to hibernating quarters. To further test these assumptions, mathematical correlations between temperature deficiencies and rainfall excesses were made against the abnormalities of leafhopper occurrence as expressed in leaf population averages above or below the normal for the five-year period. Of these comparisons the most outstanding correlations were observed between the June and July 1922 and '23 rainfall and the corresponding excesses in numbers of leafhoppers, such correlations approaching perfection; i.e., .93 with a probable error of ±.051 for June, and .96 with a ±.03 P. E. for July. Correlations of lesser weight were likewise obtained for the 1923 and '24 period by comparing excess precipitation with deficiency in leafhopper population.

Now including May in this comparison, because it is the month when the overwintering adults come out of hibernation, the temperature-rainfall interrelations are graphically shown in Graph No. X. The normal mean temperature for Erie County for the May-July period is 64.3° as shown by the heavy dotted horizontal line and the average monthly precipitation is 3.48 inches as shown by the heavy vertical line. The point at which these lines cross represents the normal mean temperature and average monthly rainfall conditions for the three months' period. The temperature-rainfall combinations for each of the years under consideration (1921-25) are represented on the diagram by circled dots for the outbreak years and circled crosses for the reduction years. The year number and total leafhopper nymph population figure (at time adults of second generation commenced to appear) is placed to the left of each circle. The years of leafhopper outbreaks (1921-23) fall well within the dry-hot portion of the diagram, indicating that such conditions are favorable to leafhopper increase. Although the circles representing the two reduction years fall below the normal temperature line, they do not cross to the wet side of the diagram. The year 1924 does approach the wet side, however, showing that the cause for leafhopper reduction in this instance is truly an interrelation between temperatures lower than normal during the May-July period

and excess precipitation during the same interval, the latter apparently acting as an inciting factor in bringing about the beginning of such a reduction period. From this graph it appears also that temperatures of less than 64.3° F., accompanied by monthly precipitations in excess of 3.4 inches when they occur during the breeding and ovipositing season, are detrimental to the normal development of the grape leafhopper.



GRAPH X. Diagrammatic Correlation between Leafhopper Outbreak and Repression Years and Mean Temperature and Total Rainfall of the May–July Period, 1921–1925.

GRAPH XI. Diagrammatic Correlation between Leafhopper Outbreak and Repression Years and Mean Temperature and Total Rainfall of the September-October Period, 1921–1925.

The September-October or "prehibernation period" also apparently bears the same relation to yearly variations in leafhopper abundance in that a mathematical correlation of .83 (P. E., .269) was found between the September-October precipitations of the years 1920-1925 and leafhopper populations at the time of the maximum abundance of the second instar nymphs fo the following season and a correlation of .77 (P. E., .198) between the same set of precipitation records and the fifth instar populations. Graph No. XI shows these relationships

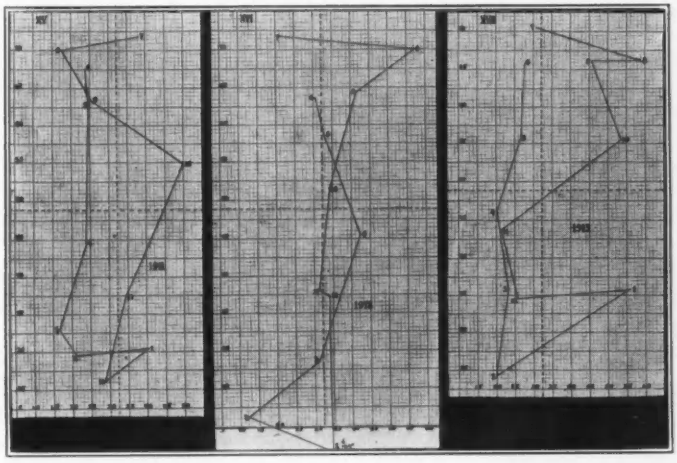
with reference to the September-October normals for the Lake Erie region and indicates that the relation at this time of the year is again closely connected with both temperature and rainfall abnormalities. The fall of 1923 was slightly lower in temperature than the preceding years (i.e., 58.5°) and the fall of 1924 slightly wetter (i.e., 3.64 inches), and these together incited the reduction or at least tended to further lower the reduction already brought about by the abnormal weather conditions already described for the spring of 1924. The fall of 1925 also adds further abnormalities, both with regard to deficient temperature (55.5°) and rainfall excess (5.56 inches), and tends to further still more the downward trend of leafhopper abundance. Here again the critical rainfall point appears to be in the general proximity of 3.5 inches, while the critical fall temperature of 58.5°, as shown by the year 1923, is a few degrees lower than the critical temperature already cited for the spring months (64.3°).

In both of the graphs just described the three points illustrating conditions during outbreak years and the two points illustrating years of abnormally low populations are too few in number to allow the drawing of accurate "trend lines." If such are approximated, however, they may be seen to run at right angles to each other and to intersect, in the case of the May-June-July graph, near the critical temperature point of 64° and in the September-October diagram slightly beyond the critical rainfall point of 3.5 inches.

To determine the effect of July temperatures and precipitations as "lag" factors in influencing leafhopper populations of the following spring, a diagram similar to Graph No. XI was constructed combining the July temperature and rainfall points for the years 1920 to 1924 with those of May and June of each following year. The graph was so similar to Graph X that it is not figured but it should be mentioned that the location of the yearly points with reference to the normal temperature axis tended to further substantiate the assertion already made that the critical spring temperature for the leafhopper is in the neighborhood of 64° F.

V. A Comparison of the Weather Conditions Described as Influencing Leafhopper Populations of 1920-1925 with Those of Other Outbreaks.

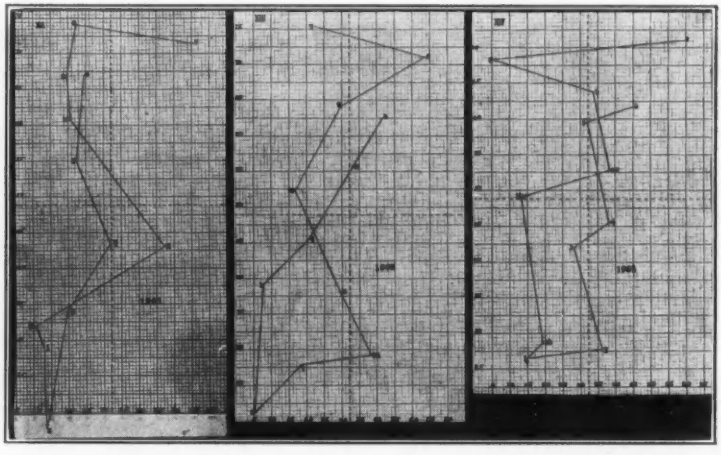
Owing to the great variation in the prevalence of parasites, predators and restraining influences other than weather factors in the different regions included in the normal geographic range of the grape leafhopper and because accurate data regarding these factors was unobtainable, it was decided to



GRAPHS XII–XIV. Temperature-rainfall Hytherographs for Leafhopper Outbreak and Repression Period, 1901–1903.

limit our comparison, for the present, to other leafhopper outbreaks and repressions occurring in the Lake Erie Region in years previous to the 1920-1925 peroid. Accurate accounts of two such phenomena are given by Johnson (2) and Hartzell (18), and these have already been discussed in the literature review at the beginning of this paper. The first of these consisted of a leafhopper outbreak commencing in 1901 and terminating in a repression year in 1903; the second outbreak occurred in 1911 and was followed by a period of greatly reduced abundance in 1913. Graphs Nos. XII to XIV illustrate in hytherograph form the weather conditions prevailing from 1901 to 1903. In Graph XII for the outbreak year of 1901 it may be seen

that the spring trend was characteristically dry during May and June, as was also the fall trend of the preceding year (1900) during September and October. The excess precipitation of July 1901 evidently came too late to cause any noticeable reduction because both Hartzell (10), and Slingerland (12), record them in immense numbers in the fall of 1901. The year 1902 (Graph XIII) was a "transition" year with a dry fall trend (1901) and a spring trend tending slightly toward



GRAPHS XV–XVII. Temperature-rainfall Hytherographs for Leafhopper Outbreak and Repression Period, 1911–1913.

excessive moisture. The reduction year (1903, Graph XIV) becomes exceedingly wet during the month of July and shows slightly heavier than normal precipitations in September and October. The spring trend supplies the climax to an unfavorable leafhopper period with abnormalities in both temperature and rainfall (i.e. mean temperature of June, 4° below normal and average precipitation, .8 inches above normal). The reduction brought about during this year was so effective that leafhoppers were not abundant in Erie County again until 1910, Johnson (2 and 19).

The second outbreak period (Graphs XV-XVII) which reached its maximum in 1911 offers a close parallel to the 1901-03 phenomena. The outbreak year (XV) opens the series

with a dry fall trend during August and September and an exceedingly dry spring trend for all months from February to June. Temperatures were about normal. The transition year (1912, Graph XVI) supplies a fall trend of slightly excessive rainfall (August, September and October) and a wet spring trend with the exception of June which crosses again to the "drier than normal" side. Temperatures during the fall trend were about normal although, as noted by Hartzell (18) January and February temperatures were excessively low. From June, 1912, however, exceedingly abnormal weather conditions prevailed (as noted by Hartzell (18), in which the subnormal temperatures of June, July, August and September were accompanied by excess precipitation, particularly in August, September and October. This year was so unfavorable that the leafhoppers failed to produce a second generation (Hartzell (18) and Johnson (2)).

CONCLUSIONS.

The foregoing study, although including a consideration of a limited number of leafhopper outbreaks in a restricted geographical area, clearly indicates that the seasonal fluctuations in population, during the years studied (1921-25), were in all probability occasioned by weather conditions, particularly temperature and precipitation. The conclusions reached concerning the exact relation of these factors to the seasonal occurrence of the leafhopper may be summarized as follows:

1. Variation in abundance and periodicity of the leafhoppers with relation to temperatures and rainfall immediately attending their seasonal activities: In the establishing and maintaining of a definite seasonal population through the medium of the first generation, temperature bears a direct relation to the time of occurrence of the normal events in the seasonal cycle (e.g., emergence from hibernation, oviposition, and rate of development of the nymphal instars), high temperatures hastening these events and low temperatures retarding them. As has been demonstrated for the Codling Moth by Isely and Ackermann (25), and for other insects, the grape leafhopper requires a certain sum total of spring temperatures, above a definite mean, to successfully complete each of the periodic events of its seasonal cycle and until these necessary temperature requirements are supplied the development of the

first generation and the occurrence of subsequent generations are necessarily delayed. The mean effective or critical temperatures for each of these events can only be determined from laboratory experiments under controlled conditions, but our observations and analyses of outbreak and repression periods lead to the belief that spring temperatures exceeding 65° F. are necessary for the normal development of the insect and temperatures between 65° and 70° are necessary to insure a steady march of the periodic events of its seasonal cycle.

In this same connection, rainfall bears a direct relation to the ability of the leafhopper to establish and maintain itself in each of its periodic changes, light precipitation apparently favoring the successful establishment of high populations and excessive or heavy precipitation being detrimental to the same. Heavy precipitations exert a marked restraining influence on the adults emerging from hibernation, on their mating and oviposition activities, and on the early nymphal stages, particularly of the first generation.

2. The relation of monthly temperatures and precipitations, particularly of the spring and fall months, to leafhopper populations during outbreak and repression periods:

A comparison of climographs or hytherographs which represent the successive average monthly temperature and rainfall conditions during outbreak or repression years indicates that years of severe outbreaks are preceded by and associated with dry spring trends of the particular season concerned and dry fall trends of the preceding season. When the reverse weather conditions occur, periods of repression take place.

When these influences in the spring and fall trends are analyzed month by month by means of mathematical correlations, the month of June of the spring trend and the months of July, September, and October of the fall trend have the greatest significance.

Further comparison and correlation by means of meteorological graphs (i.e., X and XI) in which the temperatures and precipitations for the May-June and September-October periods are expressed in deviation from the normal reveals that leafhopper outbreaks occur well within the limits of the hot-dry portion of the diagrammatic analysis and that the repression years either fall well below normal temperature conditions or pass toward the wet portion of the diagram, or lie on trend lines inclining toward either or both factors. This method of

analysis further supports the assertion that spring temperatures (May and June) of less than 64° F. are unfavorable for leafhopper development and that these same temperatures are even more unfavorable when accompanied by monthly precipitations greater than 3.5 inches. Fall temperatures (September and October) below 58.5° F. are likewise detrimental and this condition is further accentuated when they are associated with rainfall in excess of 3.5 inches.

3. By a comparison of the weather conditions which were found to influence leafhopper fluctuations during the particular period studied by the author (1921-1925) with those of earlier outbreaks in the same region (i.e., 1901-03 and 1911-13) through a study of their respective hytherographs, it was found that the same principles underlying the 1921-25 outbreak and repression phenomenon applied to these earlier occurrences; i.e., outbreaks were, in general, associated with years having warm fall and spring trends accompanied by deficient rainfall, while repressions occurred during years of cool, moist spring trends, these being frequently further associated with subnormal temperatures and excessive precipitations during the preceding fall.

BIBLIOGRAPHY.

1. **Cook, W. C.,** Unpublished lectures in Insect Ecology, University of Minnesota, 1927. (Also in Wardle, R. A., Problems of Applied Entomology, 1929.)
2. **Johnson, Fred,** U. S. D. A. Bul. 19 (Prof. Paper), 1914.
3. **Fitch, Asa,** Seventh Report N. Y. State Entomologist, 1861–62.
4. **Bethune, C. J.,** Canadian Farmer, 1868.
5. **Saunders, W.,** Ann. Report Ent. Soc. of Ontario, 1871–72.
6. **Cook, A. J.,** Thirteenth Ann. Report Sec. of Agr., Michigan, 1874–75.
7. **Lintner, J. A.,** Vineyardist, May, 1888.
8. **Lockhead, W.,** 30th Ann. Report Ent. Soc. of Ontario, 1898; 31st Ann. Report Ent. Soc. of Ontario, 1900.
9. **Felt, E. P.,** Bul. 37, U. S. D. A., Div. Ent., 1902.
10. **Hartzell, F. Z.,** Y. Y. S. Exp. Sta. Bul. 331, 1910; Y. Y. S. Exp. Sta. Bul. 344, 1912.
11. **Fletcher, J.,** 33rd Ann. Report Ent. Soc. of Ontario, 1903.
12. **Slingerland, M. V.,** Cornell U. Agr. Exp. Sta. Bul. 215, 1904.
13. **Gibson, A.,** Report Ent. Soc. of Ontario, 36, 1906.
14. **Symons, T. B.,** Yearbook, U. S. D. A., 1906; Yearbook, U. S. D. A., 1907; Yearbook, U. S. D. A., 1908.
15. **Gibson, A.,** Report Ent. Soc. of Ontario, 41, 1911.
16. **Sill, W. H.,** Pa. Dept. Agr. Bul. 217, 1912.
17. **Johnson, Fred,** Report No. 17, Pa. Dept. of Agr., 1911.
18. **Hartzell, F. Z.,** N. Y. S. Exp. Sta. Bul. 359, 1912.
19. **Johnson, Fred,** U. S. D. A. Bul. 97, 1911.
20. **Hartzell, F. Z.,** N. Y. Dept. Agr. Bul. 79, 1916.
21. **DeLong, D. M.,** Jl. Ec. Ent. 16, 1923.
22. **Van Dine, D. L.,** Jl. Ec. Ent. 16, 1923.
23. **Ross, W. A.,** 52nd Report, Ent. Soc. of Ontario, 1922.
24. **Tehon, L. R.,** Ill. Nat. Hist. Survey, Bul. XVII, Art I, 1927; Ill. Nat. Hist. Survey, Art. IX, 1928.
25. **Isely and Ackermann,** U. of Ark. Bul. 189, 1927.

THE BLUEBERRY MAGGOT FROM AN ECOLOGICAL VIEWPOINT.

F. H. LATHROP AND C. B. NICKELS,
Bureau of Entomology, United States Department of Agriculture.

It often happens that fundamental principles of ecology underlie problems of insect control, and in attacking an economic project the entomologist frequently finds himself working more or less in the field of applied ecology. Few instances in economic entomology emphasize broad ecological relationships more distinctly than does the blueberry maggot* problem.

Along the northeastern coast of Maine there has evolved during the past 50 or 60 years an industry which today furnishes an important source of livelihood for a considerable portion of the local population, and is said to produce an income of more than a million dollars annually. Yet this industry of producing blueberries has developed largely without scientific study or direction. The blueberry land is essentially wild land from which the forest cover has been removed, and it receives little or no care except for more or less haphazard mowing of the weed bushes and burning-over every third year. The blueberry plants have come onto this land entirely by their own powers of dissemination. In fact, the entire blueberry industry of northeastern Maine has evolved so naturally and blends so perfectly into the local natural economy that it gives the impression of being a step in a grand ecological succession rather than a product of commercialized agriculture.

CLIMATE AND TOPOGRAPHY.

The studies upon which this discussion is based were concentrated especially within the section of Washington County, Maine, lying approximately between the townships of Cherryfield on the west and Machias on the east, and extending some 20 or 25 miles north and south. However, in a general way the observations apply to the blueberry land of the costal section of Maine from Portland to Calais.

**Rhagoletis pomonella* Walsh; Diptera, family Trypetidæ.

The climate of this section of Maine is characterized by long, severe winters and by short, mild summers, which, in comparison to the winter climate, seem quite warm. There is usually much snow during the winter months, and during the summer months there is frequent fog, mist, and rain. The monthly mean temperatures and precipitation are shown in Table I.

TABLE I.

NORMAL TEMPERATURE AND PRECIPITATION, EASTPORT, MAINE.*

Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
MEAN TEMPERATURE.												
20.4	21.5	28.9	39.0	47.7	55.1	60.4	60.7	55.8	47.5	36.7	26.3	41.7
MEAN MAXIMUM TEMPERATURE.												
48	45	49	62	74	80	85	81	77	69	57	50	80
MEAN MINIMUM TEMPERATURE.												
—9	—5	5	20	33	41	47	48	39	29	15	—2	—13
NORMAL PRECIPITATION.												
3.92	3.35	3.83	2.84	3.01	2.97	3.08	3.00	2.78	3.55	3.32	3.74	39.39

The locality lies in the "Transition Life Zone" (*4*) and has a growing season of 120 to 150 days between killing frosts. (*11.*)

The blueberry land of this locality ranges in elevation from a little above sea level to an altitude of about 250 feet. It consists of moderately sloping to steep rocky hillsides, or of fairly level plateau areas. The typical "blueberry barrens" or "plains" are located on the plateau land.

The soil is mostly of a sandy nature, with a surface layer of dark colored organic matter. The terrain shows the effects of extreme glaciation. The surface of the soil is usually exceedingly rough, and is often studded with bowlders and rock outcrops.

The forests that originally occupied this land have been removed, largely by lumbering operations, but in some cases,

*Data furnished by U. S. Weather Bureau Station, Eastport, Maine.

according to local tradition, forest fires were started deliberately to remove the trees and promote the growth of blueberries. The present vegetation of the blueberry land consists of rather irregular stands of blueberries, which usually grow from 6 to 12 inches high, and more or less numerous weed bushes, some of which may attain a height of 6 feet or more.

THE PROCESS OF BURNING OVER THE BLUEBERRY LAND.

From an ecological viewpoint as well as for horticultural reasons, the burning-over of the blueberry land is such an important feature of the blueberry economy that the process deserves somewhat detailed consideration.

On bright, calm days in early spring, after the snow leaves, but before the frost starts out of the ground, and while the blueberry plants are still thoroughly dormant, the surface litter is ignited (Plate II, A) and under favorable conditions fire sweeps the land clean of vegetation. (Plate II, B.)

On most of the better types of blueberry land the birch, willow, and alder "sprouts" are mowed during the fall preceding burning, and there is an increasing practice of spreading a light covering of hay (Plate II, A) on the land in the fall just after the sprouts have been cut. The hay increases the amount of combustible matter on the soil and insures more thorough destruction of the surface vegetation.

THE REACTION OF THE BLUEBERRY PLANT TO BURNING.

The above-ground parts of the blueberry plants are removed by the process of burning. The root system is unharmed by the fire, and the plant responds by a greatly accelerated vegetative growth during the summer immediately following the burn, but the plant produces no fruit during this first season. During the second summer a large crop of berries is produced. (Plate I, C, D.) After this first, abundant crop the production of fruit decreases each season until the yield becomes practically nothing; unless the land is again burned-over to rejuvenate the blueberry plants. In practice, the commercial blueberry growers have found that two crops of berries between burns are all that the average land will produce profitably, and the three-year cycle usually keeps the weed bushes fairly well under control.

THE EFFECT OF BURNING UPON THE BLUEBERRY MAGGOT.

It has often been observed that the blueberries of the first crop produced after the land is burned-over usually exhibit a considerably lower degree of infestation of maggots than does the second crop. This seemed to indicate that the heat produced by the flames passing over the blueberry land destroyed a considerable proportion of the puparia in their winter quarters in the soil. A careful investigation revealed the fact that the

TABLE II.

DEPTH OF PUPATION OF THE BLUEBERRY MAGGOT, CHERRYFIELD, MAINE, 1926.

Depth	Number of Puparia	Percent	Accumulated Percent	Depth	Number of Puparia	Percent	Accumulated Percent
Surface.....	78	1.08	1.08	13th half inch	0	0	.....
1st half inch	5,235	72.71	73.79	14th " "	0	0	.....
2nd " "	1,651	22.93	96.72	15th " "	0	0	.....
3rd " "	191	2.65	99.37	16th " "	4	.06	100.00
4th " "	31	.43	99.80	17th " "	0	0	.....
5th " "	7	.10	99.90	18th " "	0	0	.....
6th " "	2	.03	99.93	19th " "	0	0	.....
7th " "	1	.01	99.94	20th " "	0	0	.....
8th " "	0	0	.....	21st " "	0	0	.....
9th " "	0	0	.....	22nd " "	0	0	.....
10th " "	0	0	.....	23rd " "	0	0	.....
11th " "	0	0	.....	24th " "	0	0	.....
12th " "	0	0	.....	TOTAL.....	7,200	100.0	100.00

puparia of the blueberry maggot occur at a shallow depth; (Table II) but, even so, the puparia in their winter quarters under the surface of the cold, moist soil are effectively protected against injury, for the fire, which sweeps quickly over the land, is not sufficient to raise the temperature of the surface soil more than a very few degrees.

The process of burning-over the land exerts practically no direct effect upon the blueberry maggot. However, the reactions of the blueberry plant to the burn profoundly influence the behavior of the maggot. (Figs. 1 and 2.)

During the summer immediately following the burn there is a normal emergence of blueberry flies (Fig. 2, 1928) on the burned-over areas, and the absence of a crop deprives the

flies of berries in which to oviposit. This may be of little consequence on small patches, but where large areas are burned-over the flies must migrate considerable distances if they are

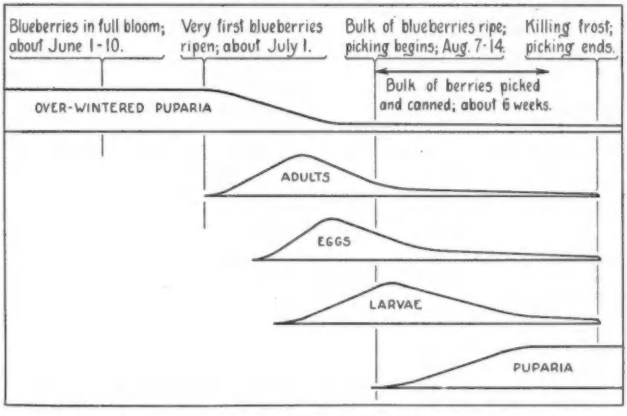

Blueberries in full bloom; about June 1-10.
Very first blueberries ripen; about July 1.
Bulk of blueberries ripe; picking begins; Aug. 7-14.
Killing frost; picking ends.
Bulk of berries picked and canned; about 6 weeks.
OVER-WINTERED PUPARIA
ADULTS
EGGS
LARVAE
PUPARIA

FIG. 1. Diagram showing life history of the blueberry maggot at Cherryfield, Maine.

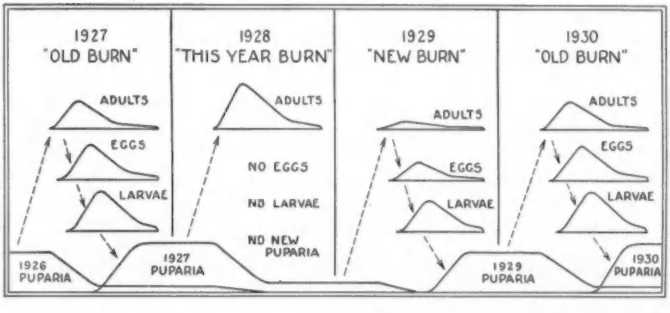


FIG. 2. Diagram showing the influence of burning upon the life history of the blueberry maggot.

to reach berries in which to oviposit. No maggots are produced on well burned land during the summer immediately following the burn (Fig. 2, 1928), with the result that the population of the species is greatly reduced.

The second summer following the burn is marked by the production of the first crop of berries, usually a heavy yield. The blueberry maggot has been "starved out" during the preceding season, and the beginning of the first crop year finds the population of the species at a low potential. (Fig. 2, 1929).

TABLE III.

SUMMARY OF EMERGENCE RECORDS OF ADULTS OF THE BLUEBERRY MAGGOT FROM FOUR CAGES OBSERVED FOR A PERIOD OF FOUR YEARS.

(Puparia formed in 1925.)

Year	Total Emergence	Per cent of 1926 Emergence
1926	1,113	.....
1927	219	19.68
1928	60	5.39
1929	6	0.54
TOTAL	1,398	

TABLE IV.

SUMMARY OF EMERGENCE RECORDS OF ADULTS OF THE BLUEBERRY MAGGOT FROM EIGHT CAGES OBSERVED FOR A PERIOD OF THREE YEARS.

(Puparia formed in 1926.)

Year	Total Emergence	Per cent of 1927 Emergence
1927	20,607	....
1928	1,466	7.11
1929	124	0.60
TOTAL	22,197	

There are two important sources of reinfestation of the new crop of berries: (1) migration of flies from unburned areas, and (2) carry-over of puparia in the soil from the second preceding season. Migration of flies is undoubtedly important on small burns of a few acres and near the margins of larger burned-over areas. Under usual conditions the migration of flies probably is not a very important factor on solid burns of 10 or 15 acres or more.

A number of workers have noted that a portion of the puparia of the apple maggot remain in the soil for two years

before adults emerge. In the case of the blueberry maggot, the carry-over of the puparia in the soil for two seasons was found to be considerable, (Tables III, IV, V) and is probably sufficient to account for the infestation of the first crop of blueberries subsequent to the burn. It is interesting in this connection to note that from puparia that were formed in 1925, adults emerged in decreasing numbers during each of the four summers of 1926, 1927, 1928 and 1929.

TABLE V.

SUMMARY OF EMERGENCE RECORDS OF ADULTS OF THE BLUEBERRY MAGGOT FROM TWO CAGES OBSERVED FOR A PERIOD OF TWO YEARS.

(Puparia formed in 1927.)

Year	Total Emergence			Per cent of 1928 Emergence		
	Male	Female	Total	Male	Female	Total
1928	571	507	1,078	.....	.....	.....
1929	68	61	129	11.91	12.03	11.97
TOTAL	639	568	2,207			

With favorable conditions, the maggot population builds up rapidly upon the first crop of blueberries. During the second crop year the maggot population of the area reaches its maximum numbers. The large population of maggots, together with the somewhat reduced yield of blueberries, accentuates the percentage of infestation of the berries on the "old burn" areas.

Picking of the blueberries acts as an ecological factor retarding the increase of the maggot population, for many of the maggots are removed from the land with the fruit. The influence of picking is lessened, however, by the fact that the maggots begin leaving the berries soon after the harvest begins.

THE BLUEBERRY MAGGOT IN RELATION TO PLANT SUCCESSION.

The plant succession in this locality is typical of the northeastern coniferous forest region. The principal stages in the succession are shown diagrammatically in Figure 3. If the forest cover is removed from the land, the vegetation usually reverts to the tall shrub association, which consists principally

of thickets of willow, alder, and birch. If the growth of these bushes is retarded by mowing and burning at intervals of two or three years, an artificial climax—the lowbush blueberry association—may be induced. The lowbush blueberry association consists largely of the lowbush blueberry, (*Vaccinium angustifolium*), often called locally low sweet blueberry, and the Canada Blueberry, (*V. canadense*), often known locally as

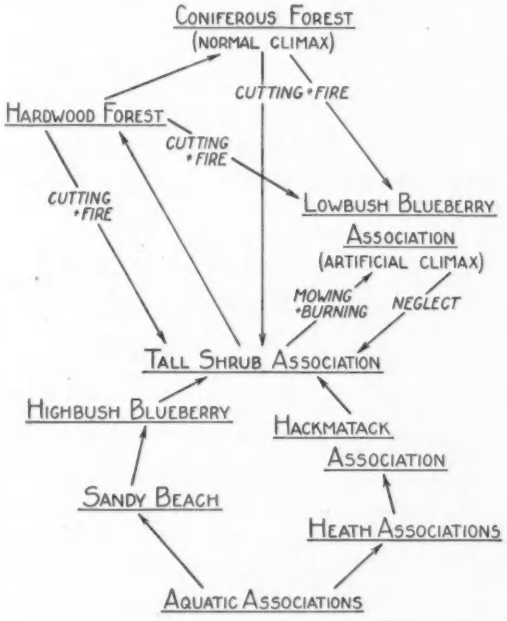


FIG. 3. Diagram showing the plant succession in relation to the lowbush blueberry association in northeastern Maine.

sourtop blueberry. Associated with these are other typical acid-soil plants such as the black huckleberry (*Gaylussacia baccata*), chokeberry (*Aronia melanocarpa*), bunchberry (*Cornus canadensis*), lambkill (*Kalmia angustifolia*), sweetfern (*Comptonia peregrina*), and sometimes the mountain cranberry (*Vaccinium vitisidaea minus*).

The population of the blueberry maggot varies considerably in different phases of the plant succession. The normal habitat

of the blueberry plant is typically a rather sparse undergrowth in the tall shrub association, and along the margins of the forest areas. Here the blueberry plants make slow growth, and comparatively few berries are produced. A considerable percentage of the berries may be infested by maggots, but, because there are relatively few plants and a scarcity of fruit, the maggot population on a unit area must remain low. A high percentage of infestation of the berries offers a favorable condition for parasitism, and the maggot population under such conditions tends to reach a rather stable equilibrium at a low potential.

When the trees and shrubs are removed from the area and the surface litter is burned off, the blueberry plants are greatly stimulated, the plants multiply and spread over the area; greatly increased yields of berries are then produced.

With the increasing numbers of berries present on the area, the parasites* of the blueberry maggot are at a disadvantage in finding infested berries in which to oviposit. Conditions favor the increase of the blueberry maggots, and the population of *Rhagoletis pomonella* on the area rises rapidly. However, the berries increase in numbers more rapidly than do the maggots, hence the percentage of infested berries decreases.

If the land receives continued care, a period arrives, after several years, when the blueberry maggot population of the area reaches a maximum (Plate IV, A). At this point the land is relatively free from weed bushes, so an excellent stand of blueberries is supported, and berries are produced in abundance. However, there still remains a sufficient growth of "sprouts" and sweetfern to furnish protection to the adult flies. If the culture is carried beyond this stage, and the sprouts and sweetfern are entirely removed from the land, there seems to be a tendency for the maggot population of the area to decrease, probably because of the excessive exposure of the adult flies to rain wind, and sunshine. Certainly, berries from blueberry land at its best development (Plate III, B) are seldom, if ever, found to have a high percentage of infestation.

If the blueberry land is neglected, (Plate IV, B) the sprouts are not mowed, and the land is not burned-over for a period of years, the vegetation soon reverts to the tall shrub association

**Opius melleus* Gahan was the most effective parasite of the blueberry maggot observed.

(Plate III, A). After a few years of neglect the yield of blueberries becomes insignificant. The percentage of berries infested by maggots may be very great, but the total population of blueberry maggots on the area is small.

SOME HOST-PLANT RELATIONSHIPS.

Rhagoletis pomonella Walsh was originally described (*12*) from a series of specimens reared in part from apple and in part from haws. The species has subsequently been reared from a considerable number of fruits, including cranberries (*8*), peach (*5*), pears (*10*), plums (*3*), Huckleberry (*Gaylussacia baccata*) (*1*), and from blueberries (*Vaccinium pennsylvanicum*, *V. canadense*, *V. vacillans*, (*13*) and *V. corymbosum* (*6*)). During the course of the investigations in Maine, the species has been reared from most of the berries found in the blueberry association, as listed below.

Blueberries:
**Vaccinium angustifolium* Kalm (m. a.)
**V. canadense* Ait. (m. a.)
**V. corymbosum* L. (m. a.)

Bunchberry:
**Cornus canadensis* L. (m. a.)

Chokeberry:
**Aronia melanocarpa* (Michx.) Britton (m.)

Huckleberry:
**Gaylussacia baccata* (Want) C. Kock (m. a.)

Mountain Cranberry:
Vaccinium vitisidaea minus Lodd (m.)

Dwarf Serviceberry:†
**Amelanchier bartramiana* Roem. (m)

Wintergreen:
Gaultheria procumbens L. (m.)

In the foregoing list there are several plants which may have considerable ecological significance. Huckleberries grow quite commonly in association with the blueberries, but usually are far less abundant than the blueberries. The huckleberries are not picked, but remain upon the plants until frost, and as they are frequently heavily infested with maggots these berries may in some places serve as an important reservoir of maggot infestation.

The bunchberry is frequently abundant on commercial blueberry land. This plant may flower and fruit every year whether the land is burned or not; hence the bunchberries are often abundant on blueberry land during the summer immediately following burning. This suggests that bunchberries may

*Plant identified by Dr. F. V. Covill, Bureau of Plant Industry, U. S. Department of Agriculture.
†Commonly known locally as sugar pear.
m. Species found infested by maggots, apparently *R. pomonella*.
a. Species from which adult flies were reared.

sustain the maggots on the burned-over land, and thus serve to increase the infestation of the new berry crop.

APPLE, HAW, BLUEBERRY RELATIONSHIPS.

From an ecological viewpoint the relationships of the forms of the apple maggot infesting apples, haws, and blueberries are most interesting. All of these fruits are infested by what is supposed to be a single species, *Rhagoletis pomonella.*

Specimens reared from blueberries are distinctly smaller in every stage than are those reared from apples or from haws. Although careful studies have been made, no definite morphological basis can be found for differentiating the two forms.

The difficulties encountered in rearing specimens of this species in confinement have prevented cross rearing and other experiments which might assist in solving the question of specific identity. In the absence of experimental rearing, other means must be used in examining the problem.

When small maggots are removed from blueberries and placed in ripe apples, the larvæ appear to feed normally. Some of the first-instar blueberry maggots transferred to apple successfully matured and formed puparia, but no adults were obtained. Of approximately 200 second-instar blueberry maggots transferred to apple, about 20 formed puparia, and 1 adult was obtained. The puparia and the adult were normal in size for the blueberry form.

Puparia were obtained from apple maggots which, in the second instar, were transferred to blueberries. No adults were obtained. The puparia were normal in size for the apple maggot. It is interesting to note that a single blueberry did not furnish sufficient food for an apple maggot, and two or more blueberries were usually consumed by each transferred apple maggot before it matured.

Evidently *R. pomonella* is a species native to the northeastern portion of the United States, where it undoubtedly infested haws, blueberries, and huckleberries before the introduction of apples by the white settlers.

That *R. pomonella* may exist upon apple independently of the blueberry, or vice versa, is suggested by the fact that the apple maggot is widespread and sometimes a serious pest in sections where blueberries and huckleberries are uncommon;

and huckleberries may be heavily infested in localities where the apple maggot is not an important pest.*

Comparable records made during the summer of 1927 indicate that the emergence of apple maggot flies averaged about seven days later than the blueberry maggot flies.

It is significant to note that there are three species of Trypetidæ of the genus *Rhagoletis* (*2*, *9*) which attack wild berries on the Pacific coast (*R. symphoricarpæ*† attacks the snowberry; *R. zephyria* and *R. tabellaria* infest the native whortleberries and blueberries), but apples are free from infestation in that region.

It seems probable that the blueberry maggot and the apple maggot exhibit an example of incipient species formation, and the present study tends to confirm the conclusion of Patch and Woods (*7*) that from an ecological viewpoint the two forms of *R. pomonella* are distinct and independent.

SUMMARY.

Few instances in economic entomology emphasize broad ecological relationships more distinctly than does the blueberry maggot problem. The entire blueberry industry of northeastern Maine has evolved so naturally and blends so perfectly into the local natural economy that it resembles a step in a grand ecological succession rather than a product of commercialized agriculture.

The climate of northeastern Maine is characterized by long, severe winters, and by short, mild summers. There is usually much snow in the winter months, and frequent fog, mist, and rain during the summer.

The blueberry land consists of rocky hillsides, or of fairly level plateau areas, all of which show the effects of extreme glaciation. The forests that originally occupied this land have been removed. The present vegetation consists of rather irregular stands of blueberries from 6 to 12 inches high, and more or

*Through the co-operation of Dr. W. J. Schoene, a sample of huckleberries was obtained from Blacksburg, Va., which was found to be heavily infested by maggots apparently similar to *R. pomonella*. Prof. J. A. Berly kindly furnished samples of huckleberries from the mountains of Oconee County, South Carolina, which were also infested with maggots apparently similar to *R. pomonella*.

†Through the co-operation of Prof. D. C. Mote, Oregon State College of Agriculture, a sample of infested snowberries and a large series of specimens of larvae, puparia, and adults of *R. symphoricarpæ* were obtained from Corvallis, Oregon.

less numerous weed bushes, some of which may attain a height of 6 feet or more.

From an ecological viewpoint as well as for horticultural reasons, the burning-over of the blueberry land is an important process. The above-ground parts of the blueberry plants are removed by the process of burning, but the root system is unharmed if the burning is done properly. During the summer immediately following the burn, the plant responds by a greatly accelerated vegetative growth. During the second summer there is an abundant crop of berries. After the first crop the production of fruit decreases each season until the yield is practically nothing, unless the plant is again stimulated by the pruning due to the burning.

The process of burning-over the land exerts practically no direct effect upon the blueberry maggot. However, the reactions of the blueberry plant to the burn profoundly influence the behavior of the maggot. During the summer immediately following the burn there is a normal emergence of blueberry flies on the burned-over areas. Because of the absence of fruit on the recently burned land no maggots are produced during the season immediately following the burn, and this condition results in a great reduction in the population of *Rhagoletis pomonella* on the area.

The second summer after the burn, marked by the production of a heavy crop of berries, finds the maggot population at a low potential. There are two important sources of infestation of this new crop of berries, (1) migration of flies from unburned areas, and (2) carry-over of puparia in the soil from the second preceding season. Records made over a period of four years indicate that the carry-over of puparia in the soil for two seasons is considerable, and is probably sufficient to account for the infestation of the first crop of berries following a burn. Flies have emerged from puparia as long as four years after the larvæ entered the soil.

With favorable conditions the maggot population builds up rapidly upon the first crop of blueberries, and reaches maximum numbers on the second crop.

The plant succession in northeastern Maine is typical of the northeastern coniferous forest region. If the forest cover is removed the vegetation reverts to the tall shrub association. If the growth of these bushes is retarded by mowing and burning

at intervals of two or three years, an artificial climax—the lowbush blueberry association—may be induced.

The population of blueberry maggots varies considerably in different phases of the plant succession. The normal habitat of the blueberry plant is typically a rather sparse undergrowth in the tall shrub association, and along the margins of the forests. Here a large percentage of the berries may be infested by maggots, but because of the relative scarcity of berries the maggot population on a unit area must remain low. A high percentage of infestation of the berries offers a favorable condition for parasitism, and the maggot population tends to reach a stable equilibrium at a low potential.

As the development of the lowbush blueberry association is induced, the production of blueberries is greatly increased. The maggot population likewise increases, but somewhat less rapidly than does the yield of blueberries; hence the percentage of infested berries tends to decrease. If the land receives continued care, a period arrives, after several years, when the blueberry maggot population of the area reaches a maximum. If the culture of the land is carried beyond this stage, the maggot population tends to decrease.

If the land is neglected, the vegetation reverts to the tall shrub association, and the maggot population per unit area decreases.

The blueberry maggot has been observed in most of the berries found in the lowbush blueberry association, including nine species.

It seems probable that the blueberry maggot and the apple maggot exhibit an example of incipient species formation, and from an ecological viewpoint the two forms seem distinct and independent.

LITERATURE CITED

(1) **Britton, W. B.** In Fifth Report of the State Ent. of Connecticut. Conn. Agr. Expt. Sta., 29th Ann. Rept. for 1905, p. 260, 1906.
(2) **Curran, C. H.** In Canadian Entomologist 56: 62–63, 1924.
(3) **Herrick, G. W.** Cornell Agr. Expt. Station Bul. 402, 1920.
(4) **Merriam, C. H.** U. S. Dept. Agr., Biol. Surv. Bul. 10, 1895.
(5) **Miller, P. H.** In Insect Pest Survey Bul. 9, No. 8, p. 325, Oct. 1, 1929.
(6) **O'Kane, W. C.** New Hampshire Agr. Expt. Sta. Bul. 171, 1914.
(7) **Patch, E. M.,** and **Woods, W. C.** Maine Agr. Expt. Sta. Bul. 308: 77–91, 1922.
(8) **Phillips, V. T.** In Jour. New York Ent. Soc. 31: 119–155, 1923.
(9) **Plank, H. K.** In Jour. Econ. Ent. 16: 99, 1923.
(10) **Porter, B. A.** U. S. Dept. Agr., Tech. Bul. 66, 1928.
(11) **Reed, W. G.** Advance Sheets 2. Atlas of American Agriculture, Part II. Climate, Section I, Frost and the Growing Season, 1918.
(12) **Walsh, B. D.** In American Jour. Hort. 2: 338–343, 1867.
(13) **Woods, W. C.** In Jour. Econ. Ent. 7: 398–400, 1914.

EXPLANATION OF PLATES.

PLATE I.

A. Blueberries in last stages of infestation by *R. pomonella*, showing shrunken condition and holes nibbled through the skin by the maggots within the berries.

B. Infested blueberries opened to show the maggots.

C. Lowbush blueberry, *Vaccinium angustifolium;* first crop of fruit after plant was burned.

D. Canada (Sourtop) blueberry, *Vaccinium canadense;* first crop of fruit after plant was burned.

PLATE II.

A. Burning-over blueberry land. This land was well mowed and the hay on the right was spread during the preceding fall. On the left the fire is shown, creeping up against the slight breeze.

B. Well burned blueberry land soon after burning, before the new growth of the plants has started.

PLATE III.

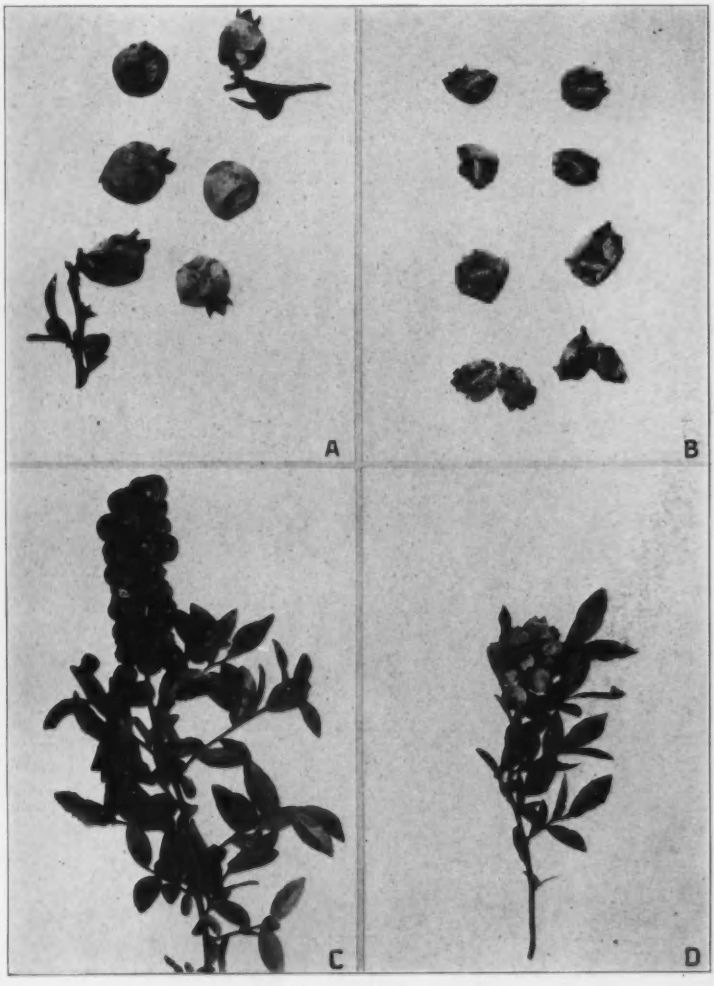
A. Neglected blueberry land that has reverted to the tall shrub association. The land is being mowed (on the right) to induce the development of the lowbush blueberry association.

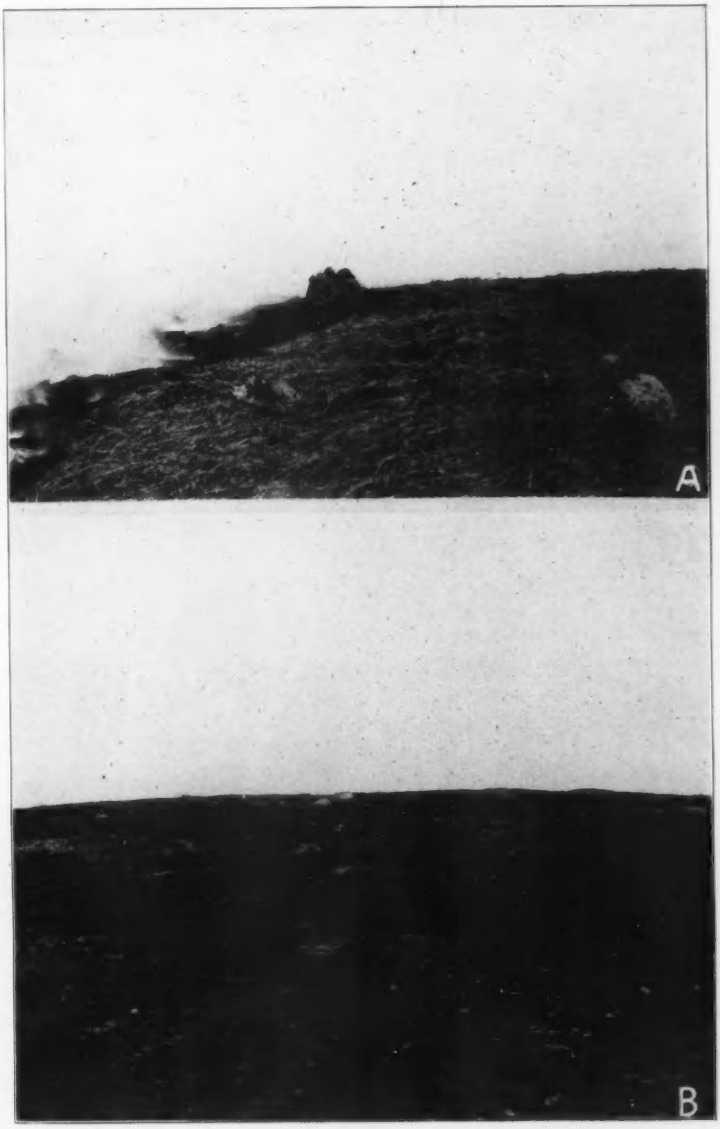
B. The lowbush blueberry association at its best. The maggot population on this type of land tends to be somewhat lower than on land with a moderate growth of birch sprouts and sweetfern.

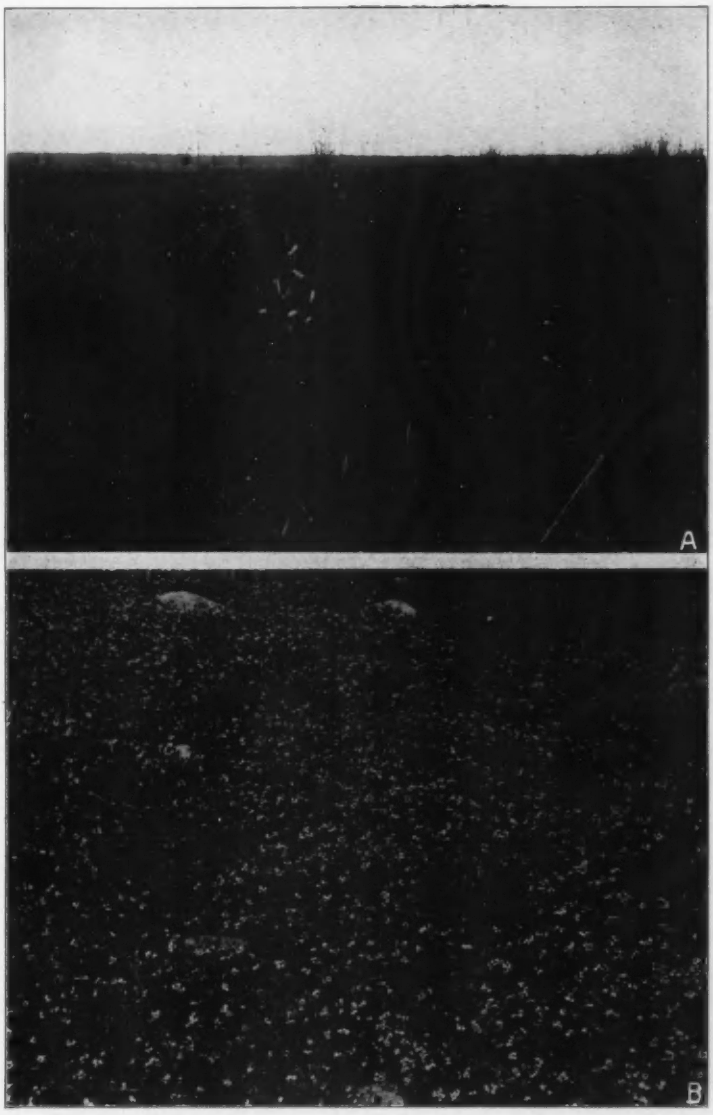
PLATE IV.

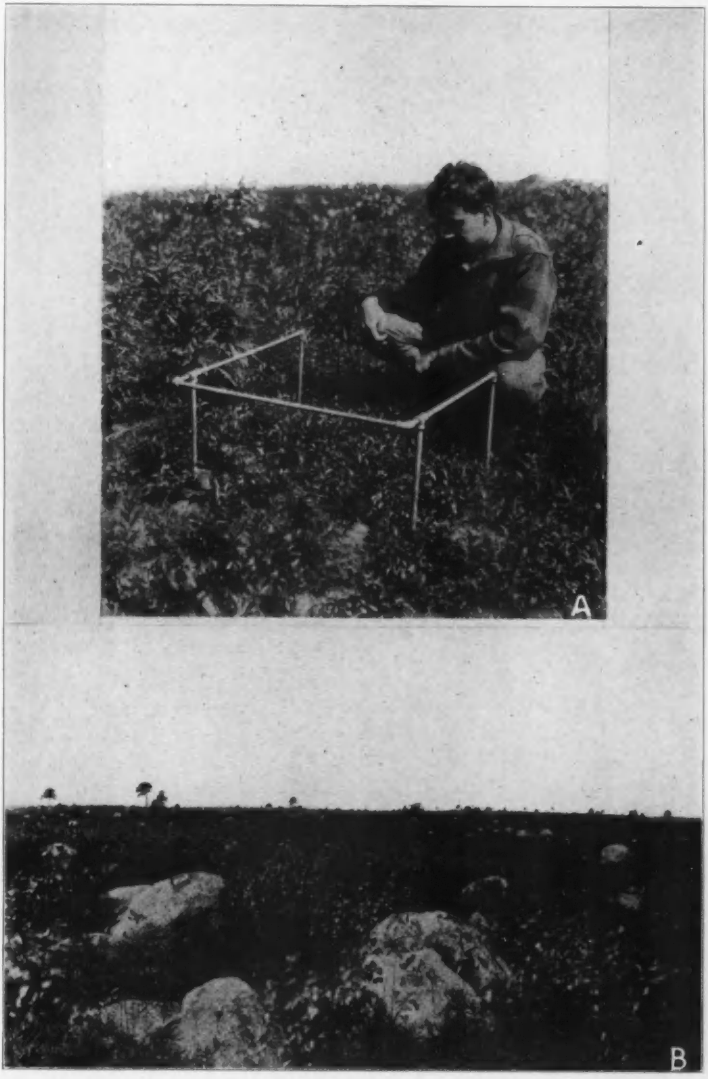
A. Blueberry land of the type that supports the maximum maggot population per unit of area. There is an excellent stand of blueberries with sufficient sweetfern and birch sprouts to furnish protection to the flies. The man in the photograph is making a count of adults on a unit area.

B. Excellent blueberry land that has been allowed to become somewhat too bushy for maximum crops of berries, or for maximum population of maggots per unit area. A high percentage of berries are infested here, and the maggot is very troublesome from a commercial standpoint.


A
B
C
D


A
B


A
B


A
B

STUDIES ON THE BIOLOGY OF PARATRIOZA COCKERELLI (SULC).*

G. F. KNOWLTON AND M. J. JANES,†
Utah Agricultural Experiment Station, Logan, Utah.

The potato psyllid was originally described and figured as *Trioza cockerelli* by Sulc (12) in 1909.

Patch (10) illustrated the wing and head of this form and mentioned the economic attention it had received in Colorado.

Crawford (4) described and illustrated this species, recorded the known range and food plants, and mentioned the fact that it sometimes became a pest of cultivated plants.

Compere (2) called attention to the injury to *Solanum capsicastrum*, caused by this insect. He (3) noted that *cockerelli* adults lived for one month in captivity; that egg-laying occurred three days after mating and continued for three days, the average number of eggs laid by the three females under observation being 36; and that in a hothouse the incubation period of eggs was 15 days. The nymphs passed through five instars, the duration of these varying from three to ten days; about 30 days were required from hatching to adult. Compere reported the broods as being continuous throughout the year at Sacramento.

Essig (5) recorded this as a minor pest in California; described the various life history stages, noting that the broods greatly overlapped; and that three to many broods occurred each year in California.

List (7, 8), recorded this as frequently becoming a tomato pest in Colorado and discussed control measures.

Richards (11) described an apparently new disease of potatoes, which he named "yellows"; this abnormality occurred during the summer of 1927 in Utah, Idaho, Montana, and Wyoming. The symptoms are described; the relationship of the nymph of *cockerelli* to this systemic disturbance is given.

*Contribution from the Department of Entomology, Utah Agricultural Experiment Station, in co-operation with the U. S. Bureau of Entomology.

†Associate Entomologist and advanced student in Department of Entomology, respectively.

Publication authorized by Director, December 5, 1930.

Binkley (1) recorded the occurrence of a destructive disease affecting potato in Colorado, thought to be associated with *cockerelli;* the disease seemingly was not produced by the feeding of the psyllids alone, but appeared to be a virus disease; nymphs hatched under sterile conditions did not produce the disturbance; the virus apparently does not pass through the egg.

Pack (9) recorded that the incubation period of *cockerelli* eggs was from 3 to 15 days and that the completion of nymphal development required from 14 to 17 days.

Recognition of the tomato psyllid as a serious pest, capable of affecting agricultural crops over a large area, followed the rather conclusive evidence obtained by Richards that the nymphs of *cockerelli* are closely associated with the development of the serious potato disturbance now known as psyllid yellows.

During the last three seasons a few areas in Utah have been affected by psyllid yellows, but the potato crop in general has not been affected in any way comparable to the serious damage of 1927. In most instances the damage to early potatoes has been much more severe than to the late potato crop.

The following life history studies were carried on in the entomological laboratory at the Utah Agricultural Experiment Station. Field studies and preliminary work on control were carried on during 1930 at the Davis County Experimental Farm at Farmington.

EGGS

The eggs of *cockerelli* are small, spindle-shaped to elongate-oval, usually shiny yellowish-orange in color, with a deeper orange on the pointed end supported by the short stipe. As fertile eggs develop and are nearly ready to hatch, the color in the basal end becomes a deeper orange, and the egg usually becomes somewhat flattened across the top, due to the flat shape of the contained nymph. Eggs are deposited on both upper and lower surfaces of the leaves and along the margins; a few have been found on the petioles and stems. Eggs are laid most abundantly on young apical leaves. Frequently a female will deposit a number of eggs in a row; in other cases she may scatter the eggs over the surfaces of two or more leaves during the course of a day. Ovipositing females usually deposited from five to 50 eggs during 24 hours; however, one female deposited 157 eggs during this interval of time. After

having laid 865 eggs between June 3 and June 26, this female escaped. During this period eggs were deposited daily except on the two days preceding the 24-hour period in which 157 were laid. During the 23 days of oviposition in captivity, this individual's daily average was 37.6 eggs.

The incubation period for eggs varied from three to nine days. The majority of the eggs hatched on the fifth and sixth days; however, during warmer weather a number hatched on the fourth day, while during cooler periods a number of eggs hatched on the seventh and a smaller number on the eighth day. Less than one per cent of the eggs hatched in less than 4 days, or required more than 8 days. Sometimes all eggs from one day's laying hatched on a given day, but usually they hatched over a period of three to four days.

Counts were made to determine the hatchability of a large number of eggs. It was observed that most of the eggs of some females were fertile, while those from other females would be largely infertile. Observations were made on 9,615 eggs, of which 7,989, or approximately 73 per cent, hatched.

In a few cases observations were made to determine the length of time a female could produce fertile eggs after the last mating. A male was placed with a female on July 31 and removed as soon as mating had been completed. Fertile eggs were deposited up to August 26; those produced thereafter were infertile. In a second case eggs deposited 24 days after mating were fertile and those produced thereafter were infertile. In a third instance all eggs deposited later than three days after mating were infertile.

NYMPHS

Just before hatching, the red eyes and sometimes the general body form of the nymph may be seen through the rather transparent egg shell. The head of the nymph is in the large apical end of the egg. The first evidence of hatching is the protrusion of the extreme anterior end of the body through the apical end of the shell, followed by the appearance of the pro-thoracic legs. At this place the nymph usually takes a short rest, after which it completely emerges. If the egg is on the upper side of the leaf, the movement during emergence partially telescopes the eggshell; while pulling the caudal end of the body from the egg, the shell is usually nearly straight-

ened out. After completing its emergence, the pale yellow and orange nymph creeps down the pedicil, moves around on the plant for a short time, then begins feeding. The time required for individual nymphs to completely emerge from the eggshell varied from 2.5 to 7.5 minutes, the average time for five individuals being 5.2 minutes.

After hatching from the egg the nymph passes through five instars. The duration of time in each stadium is somewhat variable. The length of time required in the first stadium varied from one to five days, the most frequent period being three days, with a great number requiring but two days. The average time required for 252 first-instar nymphs to complete this stadium was 2.76 days. Most of the nymphs that hatched from the eggs lived to complete the first-instar growth, but a high mortality resulted at the first ecdysis. The mortality among nymphs at the first molt was higher than for the four subsequent molts combined. The time required for completion of the second stadium varied from one to five days, the average time required for 186 nymphs being 2.44 days, or slightly less than the first-instar average. Third-instar development was completed in from one to four days, the average time required for 158 nymphs being 2.49 days. The variation in time required to complete the fourth stadium ranged from one to five days, the average time for 151 nymphs being 2.72 days, or nearly as long as the average for the first instar. More time was required in the fifth stadium than in any of the four preceding, the range being from three to nine days, with the average for 133 individuals that completed nymphal development being 4.87 days.

The length of time required to complete nymphal development varied to quite an extent, the greatest spread of all being in individuals maturing during June; one required 12 days to complete nymphal development while the development of another extended to the twenty-first day. Two individuals completed nymphal development in 19 days, but all others completed their development in 18 days or less, the minimum being 12 days. The length of time required for nymphal development in the laboratory varied with the time of year: The average number of days required during April was 16.9; during May, 17.2; during June, 15.1; during July, 13; during August, 15.45; during September, 16.1; and during October,

17 days. The average time required for the 133 nymphs to complete development was 15.35 days.

A second-instar nymph was observed to require 5 seconds for the outer cuticula to split down the back; 7 minutes were required for the nymph to completely emerge from the exuviæ.

ADULTS

The coloration of newly-emerged adults changes noticeably during the first two or three days after the adult stage is reached. The newly-emerged adult is usually pale green or light amber in color. During the first 24 hours the body becomes a darker amber; during the second 24 hours the body becomes more of a brown, with a blackish cast appearing in many individuals, followed by a darker brown to black coloring, with pronounced characteristic white powdery markings. The dark coloration is obtained in from two to five days.

The sex was determined on 127 of the individuals that completed development during the life-history studies; 62 were males and 65 females, giving a sex ratio of approximately 1 to 1.

The adult *cockerelli* is active and easily disturbed but behaves well when confined in a small clip cage on a potato leaf. The type of cage used for adult psyllids is the same as that commonly used in this area for inoculating sugar-beets with curly-top virus by means of infective beet leafhoppers. This cage is made from a 4-dram homeopathic vial, the closed end being cut off, and the cut end of the bottle wall being flanged and covered with cheesecloth. A spring clamp and a metal disc to fit against the mouth of the bottle completes the cage. The adults feed, mate, and oviposit in the cages as readily, apparently, as they do when free on the plants. The cage was moved daily to a fresh leaf.

Under laboratory conditions the length of life varies greatly. Some individuals die within a day or two after emergence, while the longest record for a male was 64 days, and for a female 189 days. Knowlton (6) recorded one female that produced 1151 eggs. The female living the longest deposited 1352 eggs over a period of 179 days. Weeks before her death, the wings of this female were worn away until little more than stumps remained. One female lived 80 days and deposited 248 eggs, while another lived 71 days and laid 876 eggs. The total

number of eggs laid by 51 females that died in cages was 16,215, with an average of 318 eggs each. Nine females escaped while still ovipositing; up to the time of their escape, these individuals had deposited 3618 eggs, or an average of 402 eggs per female. The entire group of 60 females deposited 19,833 eggs, or an average of 330.55 eggs each.

The length of the oviposition period varied greatly, some females depositing eggs for a day or two only, while one female continued producing for 179 days; however, eggs were not produced each day of the oviposition period by most females. The average oviposition period for 58 females was 21.45 days. The preoviposition period varied with different females from five to 25 days, with an average of 10.1 days from emergence until the first eggs were produced. Most females under observation died within a few days after depositing the last eggs; however, one female lived on for 24 days. The average length of life after egg-laying ceased was 4.12 days. The average length of life for 53 males was 25.22 days and that of 56 females 34.4 days. Six females died without ovipositing.

Observations were made on 10 unmated females. Five of these deposited infertile eggs in numbers from 14 to 102, with an average of 49 per ovipositing female. The oviposition period ranged from one to 25 days, with an average of 12 days. Preoviposition periods for these females ranged from four to 47 days and post-oviposition periods from three to 29 days. The five remaining females failed to oviposit.

MATING

Just previous to mating the male becomes unusually active and apparently excited. He walks up to the side of a female and works his abdomen up and down against the body of the female in an attempt to place his abdomen under her wings. When the abdomens of the two individuals come together, mating occurs with the male and female standing with heads in the same direction. The male and female may both be standing on the surface of the plant or the male may cling to the side of the female. During the mating process the psyllids stand quietly together, the principal movement observed being movements of the antennæ. Mating usually lasts for a period of several minutes. Sixteen matings were timed; these con-

tinued over a period of from 1.5 to 14 minutes, with an average of 6 minutes. Mating was observed in one pair on the fourth day after emergence. In no instance was mating observed until after the adults had obtained the characteristic dark coloration.

FIELD OBSERVATIONS

Some interesting observations were made at the Davis County Experimental Farm during the season of 1930. Early potatoes began showing psyllid yellows by the end of the first week in June; by June 20 the earliest potatoes were in a serious condition, with most plants yellowed and with many plants producing aerial tubers. At this time adult psyllids were moderately abundant, cast fifth-instar skins were common, and 166 nymphs were found on the first plant examined. The potato hill was selected as the unit of comparison. On June 21, the plants on six hills of early potatoes were examined; the nymphal infestation ranged from 74 to 1086 on these plants, with an average of 456 to the hill. At this time large numbers of nymphs were in the fifth instar and adults were becoming rather abundant. One hill of late potatoes was examined at this time and only five nymphs were found. Four hills of early potatoes examined on June 28 showed a lower population, individual hills ranging from 72 to 263 nymphs, with an average of 149 for the four hills. On July 5, the plants from eight hills were examined, the number of nymphs ranging from 0 to 22 and with an average of four nymphs to the hill. Counts during the remainder of the summer ranged from 0 to 62, with an average of about six nymphs per hill. There was an overlapping of generations during the summer.

Sweepings were made with an insect net, to determine the abundance of adult psyllids at various times during the season. The number taken increased from June 20 to a peak on June 27 and then gradually decreased, so that during the latter part of July and during August only small numbers were taken at each sweeping. The unit of measurement used in estimating adult populations was 50 sweeps with a standard 15-inch American insect net.

The adult material collected on several occasions was examined to determine the sex ratio: 494 specimens were

males and 597 females, a ratio of approximately five males to six females.

Different observers have noted that during hot, sunny weather, the majority of *cockerelli* nymphs seek the underside of the leaf. Records were kept of the distribution of the nymphs on much of the material examined during June and early July; 14 nymphs were on the petiole, 146 on the larger stems, 1549 on the upper leaf surface, and 3251 on the lower surface of the blade. Shade appeared to be the limiting factor rather than position of the leaf. When psyllids are produced in the greenhouse during the cool part of the year, the nymphs become abundant on the upper surface of the leaf and also on the stem; they may be found feeding on any of the above-ground portions of a succulent potato plant.

LITERATURE CITED.

(1) **Binkley, A. M.** Transmission studies with the new psyllid-yellows disease of solanaceous plants. *Science*, 70, No. 1825, p. 615, 1929.

(2) **Compere, H.** *Paratrioza cockerelli* (Sulc). Calif. Mo. Bul. 4: 574, 1915.

(3) **Compere, H.** Notes on the tomato psylla. Calif. Mo. Bul. 5: 189–191, 1916.

(4) **Crawford, D. L.** A monograph of the jumping plant lice of the new world. U. S. Nat. Mus. Bul. 85, pp. 71–72, 1914.

(5) **Essig, E. O.** The tomato and laurel psyllids. *Jour. Econ. Ent.* 10: 434–439, 1917.

(6) **Knowlton, G. F.** *Paratrioza cockerelli* (Sulc). Bien. Rept. 1928–1930, Utah Exp. Sta. Bul. 220, p. 42, 1930.

(7) **List, G. M.** Tests of insecticides. Ninth Ann. Rept. State Entom., Colo. State Ent. Cir. 26, pp. 40–41, 1918.

(8) **List, G. M.** The tomato psyllid, *Paratrioza cockerelli* Sulc. Sixteenth Ann. Rept. State Ent., Colo. State Ent. Cir. 47, p. 16, 1924.

(9) **Pack, H. J.** Potato psyllid. Utah Agr. Exp. Sta. Bul. 216, p. 21, 1930.

(10) **Patch, E. M.** Psyllid notes. Maine Agr. Exp. Sta. Bul. 202, p. 231, 1912.

(11) **Richards, B. L.** A new and destructive disease of the potato in Utah and its relation to the potato psylla. *Phytopathology*, 18, 140–141, 1928.

(12) **Sulc, K.** *Trioza cockerelli* n. sp. *Acta. Soc. Ent. Bohemiae* 6, 105–108, 1909.

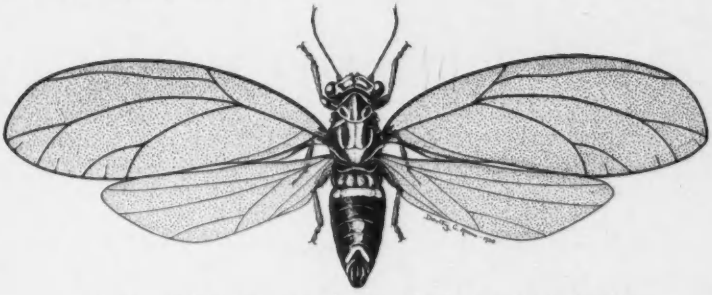


FIG. 1. Adult male potato psyllid, *Paratrioza cockerelli* (Sulc).

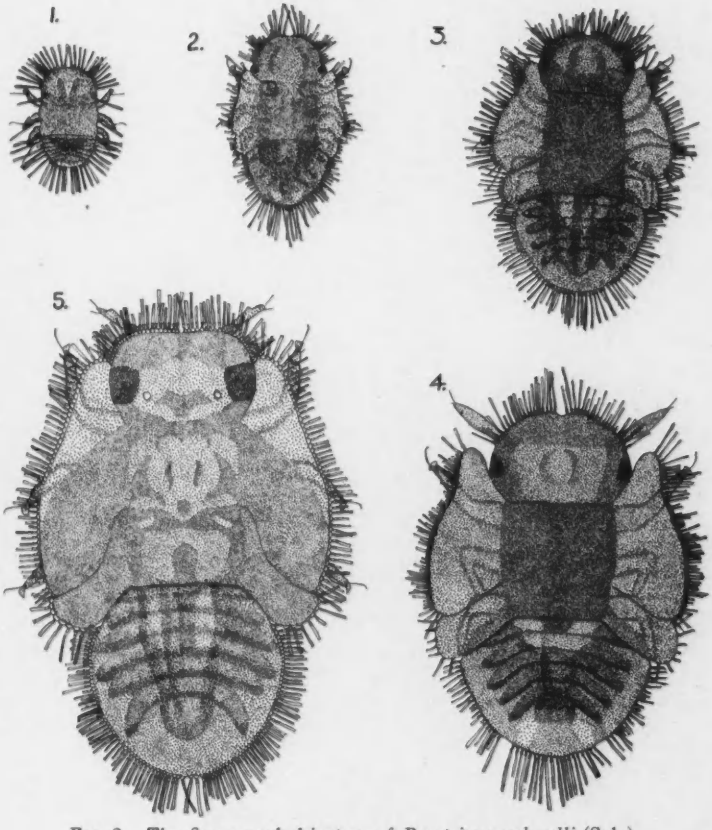


FIG. 2. The five nymphal instars of *Paratrioza cockerelli* (Sulc), showing relative size and shape.

MACROCENTRUS ANCYLIVORA ROHR. AND M. DELICATUS CRESS. DISTINCT SPECIES.*

BYRLEY F. DRIGGERS, Associate Entomologist,
and
BAILEY B. PEPPER, Temporary Assistant,
New Jersey Agricultural Experiment Station.

INTRODUCTION

The Braconid parasite *Macrocentrus ancylivora* Rohr. was described in 1923 by Rohwer (6) from specimens reared by Fink (3) from the strawberry leaf roller *Ancylis comptana* Froehl. Stearns (7) proved in cross-breeding experiments that *Macrocentrus* bred from the strawberry leaf roller and from the larvæ of the oriental fruit moth were the same species. *Macrocentrus ancylivora* Rohr. has been recorded as a parasite of the oriental fruit moth from Virginia, Maryland, Pennsylvania, New Jersey, Connecticut, New York and Ohio.

Peterson and Haeuseler appear to have been the first to note the occurrence of a species of *Macrocentrus* other than *ancylivora* on the oriental fruit moth. Peterson called the senior writer's attention to the occurrence of a light colored brood of *Macrocentrus* at Riverton in the summer of 1927. These were identified later as *M. delicatus* Cress. This species has been recorded since 1927 as a parasite of the oriental fruit moth in New Jersey, Connecticut, and New York (1, 4, 5). Previous to 1927 it is recorded as having been reared from several different hosts (2). *Macrocentrus delicatus* Cress. was reared in considerable numbers from larvæ of the fruit moth collected in localities in the northern part of New Jersey from 1927 to 1930 and also from Riverton in the southern part of New Jersey in 1927, 1928 and 1929.

The occurrence of *M. delicatus* Cress. in considerable numbers on the oriental fruit moth at several localities in New Jersey every year from 1927 to 1930 led the writers to suspect this parasite was present on the fruit moth before 1927. Thirty

*Paper of the Journal Series, New Jersey Agricultural Experiment Station, Department of Entomology.

specimens of *Macrocentrus* which had been reared from oriental fruit moth larvæ collected in different localities in New Jersey in 1925 and 1926, were found in the department insect collection. The specimens were labeled *M. ancylivora* Rohr. and the records showed they had been identified by a recognized specialist in that group of parasites. Six of the thirty specimens appeared to be *M. delicatus* and when submitted to Mr. R. A. Cushman of the National Museum they were verified by him as this species.

This past summer the writers visited a fruit moth laboratory in one of the eastern states. An opportunity was afforded to examine the *Macrocentrus* specimens on hand which had been reared from peach moth larvæ collected in that section in previous years. The specimens were labeled *Macrocentrus ancylivora* Rohr. and the records showed the source of identification was the same as that of the New Jersey material of 1925 1926. The majority of the specimens appeared to be *M. delicatus* although no careful examination was made of all the specimens. A number of cases of misidentification of species in several states similar to the above have come to the attention of the writers since this study was begun.

On several occasions one or two entomologists working on the oriental fruit moth and its parasites have expressed doubt that there are two species of *Macrocentrus* attacking the fruit moth. It was suggested that possibly *M. ancylivora* and *M. delicatus* reported from the fruit moth were color variations of the same species. During 1929 and 1930 life history studies were carried on at New Brunswick on *M. ancylivora* and *M. delicatus* using the larvæ of the oriental fruit moth as host. In addition several attempts were made to cross-breed the two species in the summer of 1930. It seemed worthwhile to present the results of these experiments at this time and to point out the difference in the two species.

METHODS

The cages used in the life history and cross-breeding work with *Macrocentrus* were cylindrical screen wire approximately 10 inches in diameter and 12 inches tall. The cages were set in pans of moist sand and the tops covered with a good grade of muslin. The parasites used in the breeding experiments were reared from oriental fruit moth larvæ collected in the field.

Each larva was placed in an individual vial so that when the parasite emerged there was no chance for it to come in contact with any other individual before being placed in the breeding cage.

The oriental fruit moth larvæ used in the breeding experiments varied in age from one to several days. They were obtained by inserting peach twigs in moth cages and as eggs were deposited the twigs were removed and set aside until the eggs had reached the black spot stage. Succulent twigs were collected in the field, the leaves removed, and placed with the twigs containing the black spot eggs. Upon hatching the larvæ entered the succulent twigs and to some extent the older twigs bearing the black spot eggs. The succulent twigs containing the newly hatched larvæ were transferred to the cage containing the parasites. The twigs were allowed to remain in the parasite cage from 24 to 48 hours, after which they were removed and placed on apples in battery jars with strips of corrugated paper. The larvæ came out of the twigs and entered the apples where they completed their growth. The battery jars were examined daily for larvæ that had spun cocoons in the straw paper corrugated strips. These were removed and placed one in a vial for further observations.

The apples used in the breeding work were collected as needed from a tree near the insectary. Succulent peach twigs were also collected as needed from young trees in an adjoining orchard. An effort was made to collect only twigs and apples free of larvæ. However, there was always the possiblility that a few recently entered larvæ would escape notice and be included in the life history material. Since *Macrocentrus* parasitizes larvæ in all stages of development it is probable that a small percentage of the parasites obtained in the breeding experiments were from larvæ parasitized in the field before they reached the breeding cages.

LIFE HISTORY NOTES IN 1929 AND 1930

The life history study of *M. delicatus* was begun in the insectary at New Brunswick on July 13, 1929 and a similar study on *M. ancylivora* on July 26, 1929. The two studies were continued to the end of the season. Those larvæ that failed to complete their development in the fall were carried over the winter. Thirty-one individuals of *M. delicatus* and

110 *M. ancylivora* completed the life cycle from egg to adult emergence in the period from the time the experiments were begun in July to the end of the season. The average number of days for all generations in the cycle of *M. delicatus* was 32.2 and *M. ancylivora* 35.5.

Enough individuals of *M. ancylivora* survived the winter to enable us to continue the life history study of this species from the beginning of the season of 1930. Accordingly the first generation of *M. ancylivora* was begun May 14, 1930 using adults that had emerged in the insectary. The studies were continued throughout the season and a total of 735 individuals completed the life cycle. We did not succeed in carrying over the winter *M. delicatus*, therefore the life history study of this species was suspended until adults could be reared from larvæ collected in the field. The life history study of *M. delicatus* was resumed July 17, 1930. From that date to the end of the season 301 individuals completed their life cycle. The average number of days in the life cycle of *M. delicatus* and *M. ancylivora* from July 17 to the end of the season of 1930 was 35.6 and 35.2 respectively. A considerable number of individuals of both species emerged as late as November. These late emerging individuals required from 40 to 70 days to complete the cycle.

It had been observed that the light colored *Macrocentrus*, which were thought to be *delicatus*, were reared from larvæ collected in the field about the time second brood fruit moth larvæ were appearing. *Macrocentrus* individuals reared from larvæ collected early in the season of the first brood were of a dark orange color and were believed to be *ancylivora*. Careful watch was kept on the individuals emerging from one generation to the next in the life history studies of both species to see if there was any pronounced color change. There was no noticeable change. The light yellow *delicatus* produced light colored progeny from one generation to the next and the dark orange *ancylivora* likewise ran true in respect to color. There was a difference however in the proportion of sexes between the two species, *ancylivora* tended to produce more females than males whereas *delicatus* produced more males than females. Seventy-two per cent of the *ancylivora* were females in 1929 and 60 per cent females in 1930. The *delicatus* material ran 75 per cent males in 1929 and 74 per cent males in 1930.

ATTEMPTS TO CROSS-BREED THE TWO SPECIES

Attempts to cross-breed the two species were made beginning the latter part of July, 1930, when there was a maximum number of individuals of both species emerging in the life history and field collected material in the insectary. Four cages were made up similar to those used in the life history studies. Parasites that had recently emerged in individual vials were used in stocking the cages. July 22, 8 female *ancylivora* were liberated in cage 1; in cage 2, 7 female *delicatus* were liberated; cage 3 received 6 female *ancylivora* and 9 male *delicatus* and to cage four was added 5 female *delicatus* and 5 male *ancylivora*. Observations were made to see if any copulation took place. None was observed although copulation occurred in adjacent life history cages containing the two sexes of the same species. The following day batches of twigs containing recently hatched larvæ were inserted in each of the four cages. At the end of 48 hours the twigs were removed from the cages and placed in battery jars on apples to complete their growth. From this point on they were handled in the same way as described in the life history methods.

From the larvæ exposed to the unmated *ancylivora* females in cage one 13 males with the typical *ancylivora* markings emerged. From cage 2 (unmated *delicatus* females) there emerged 18 males with the typical *delicatus* markings. Cage 3 (*ancylivora* females and *delicatus* males) produced nine males and one female of typical *ancylivora* characteristics. Cage 4 (*delicatus* females and *ancylivora* males) produced seven male *delicatus*.

The above experiment was repeated July 30-August 1 with the following results. Cage 1 (unmated *ancylivora* females) produced 10 males and 1 female having the typical *ancylivora* markings. Cage 2 (unmated *delicatus* females) produced 18 males with the typical *delicatus* markings. Cage 3 (*ancylivora* females and *delicatus* males) produced 12 male *ancylivora*. No parasites emerged from the larvæ exposed to *delicatus* females and *ancylivora* males in cage 4.

August 5 to 8, 1930 a third experiment was run. *Ancylivora* females crossed with *delicatus* males produced 4 male *ancylivora*. The *delicatus* female and *ancylivora* male cross in the third experiment producing no progeny. A fourth experiment from

August 26 to 29 produced ten *delicatus* males from a cage containing *delicatus* females and *ancylivora* males. A fifth and last experiment was set up September 7 to 10. *Ancylivora* females and *delicatus* males produced 4 *ancylivora* males. *Delicatus* females and *ancylivora* males produced 4 *delicatus* males.

The adult *Macrocentrus* used in the five attempts at cross-breeding during July, August and September, 1930, were carefully labeled and preserved. Likewise the progeny resulting from these attempts at crossing were carefully labeled as to source. Examination of the material showed that those females possessing *delicatus* characters produced only males with *delicatus* characters whether the females had access to males having *ancylivora* characters or not. Also the females possessing *ancylivora* characters produced only males with *ancylivora* characters with two exceptions. In the *ancylivora* female and *delicatus* male cross in the first experiment 13 males and 1 female *ancylivora* were produced and the unmated female *ancylivora* in the second experiment produced 10 males and 1 female *ancylivora*. On the face of the evidence it would appear that *M. ancylivora* is deuterotokous. However it will be recalled that the twigs and apples used in rearing the larvæ were collected from trees where peach moths and parasites were prevalent. Therefore the two female *ancylivora* probably came from young and already parasitized larvæ present in the twigs or apples at the time they were collected. All of the parasites used in the attempts at cross-breeding and the progeny resulting were submitted to Mr. Cushman who wrote that the determinations appear correct.

MORPHOLOGICAL DIFFERENCES

Mr. R. A. Cushman identified the *Macrocentrus* material sent to the U. S. National Museum from the New Jersey Experiment Station since 1927. The following characters for distinguishing *delicatus* from *ancylivora* were supplied by Mr. Cushman in a letter to the senior author.

"In *ancylivora* the stigma is relatively shorter and broader with the radius not far beyond the middle and it is more or less stained with a dark color. In *delicatus* the stigma is long and narrow with the radius far beyond the middle and it is entirely pale straw-colored. As a checking character one might use the

number of joints of the antennæ; in *ancylivora* there are 41-46 joints and in *delicatus* 51-56 joints."

Besides the foregoing characters the writers, in handling hundreds of specimens of both species in the insectary, have observed other differences, some of which were used for separating live material in the insectary. The ground color of the body of *delicatus* is pale straw-colored with the dorsal aspect of the thorax and abdomen in some specimens dark. The ground color of *ancylivora* is dark orange or brownish red. This agrees in general with Cresson's "pale honey-yellow" for *delicatus* and Rohwer's "ferrugineous" for *ancylivora* in the original descriptions. The antennæ of *delicatus* are longer than *ancylivora* and in *delicatus* the points of articulation of the joints of the antennæ are darker than the rest of the joint, giving the antennæ a beaded appearance when observed with a hand lens or the naked eye. This beaded effect is not evident in the antennæ of *ancylivora*. When specimens of *delicatus* are killed and mounted on pins the tips of the antennæ tend to curl so as to form one or more loops. The curl at the tips of the antennæ of *ancylivora* is not as pronounced as that of *delicatus*.

The points used in separating two species rapidly in the insectary were (1) the general color—pale yellow in *delicatus* and dark orange in *ancylivora;* (2) appearance of antennæ—beaded in case of *delicatus* and hair-like in case of *ancylivora* and (3) color and shape of stigma—pale yellow, long and narrow in *delicatus* and dark brown to black and short and broad in *ancylivora*. The length and number of joints in the antennæ and the position of the radius in respect to the stigma were used for further checking after the parasites were mounted.

Figures one to four, Plate I, are illustrations of the two sexes of *M. ancylivora* and *M. delicatus*. The authors are indebted to Mr. B. Landis of Ohio State University for assistance in the preparation of the drawings.

SUMMARY AND CONCLUSIONS

The parasite *Macrocentrus ancylivora* Rohr. was first reared and described in 1923 from the strawberry leaf-roller. Later it was reared from larvæ of the oriental fruit moth. Another species identified later as *M. delicatus* Cress was first noticed by Peterson and Haeussler in 1927. Both species were found

parasitizing the larvæ of the oriental fruit moth in New Jersey from 1927 to the present and there is evidence that *M. delicatus* was active as a parasite of the fruit moth before 1927.

Different determinations as to species have been made of *Macrocentrus* specimens reared from the oriental fruit moth and several entomologists carrying on investigations of this pest and its parasites have expressed doubt that there are two species of *Macrocentrus* attacking the fruit moth. It has been suggested that possibly what appeared to be two species was merely color variations of the same species.

Life history studies carried on in 1929 and 1930 and attempts to cross-breed the two species in 1930 produced data which seem to prove that *Macrocentrus ancylivora* Rohr. and *Macrocentrus delicatus* Cress. are two distinct species parasitizing the larvæ of the oriental fruit moth. Morphological differences between the two species are discussed.

LITERATURE CITED.

(1) **Driggers, B. F.** 1929. Some Parasites of the Oriental Peach Moth in New Jersey. Jour. N. Y. Ent. Soc., Vol. 37, p. 171.
(2) **Driggers, B. F.** 1930. Some Studies on the Larval Parasites of the Oriental Peach Moth (*Laspeyresia molesta* Busck.). N. J. Agr. Expt. Station Bulletin 510.
(3) **Fink, D. E.** 1926. The Biology of *Macrocentrus ancylivora* Rohwer, an Important Parasite of the Strawberry Leaf Roller (*Ancylis comptana* Froehl.). Jour. Agr. Res. 32: 1121–1134.
(4) **Garman, P.** 1930. The Oriental Peach Moth in Connecticut. Conn. Agr. Expt. Station, Bulletin 313.
(5) **Haeussler, G. J.** 1930. Parasites of the Oriental Peach Moth *Laspeyresia molesta* Busck., in North America. Jour. Agr. Res. 41: 365–377.
(6) **Rohwer, S. A.** 1923. A New Macrocentrus Reared from the Strawberry Leaf Roller. Proc. Ent. Soc. Wash. 25: 168.
(7) **Stearns, L. A.** 1928. The Larval Parasites of the Oriental Peach Moth (*Laspeyresia molesta* Busck.) with special reference to the Biology of *Macrocentrus ancylivora* Rohwer. N. J. Agr. Expt. Station, Bulletin 460.

EXPLANATION OF PLATE.

Fig. 1. Male of *Macrocentrus ancylivora*.
Fig. 2. Male of *Macrocentrus delicatus*.
Fig. 3. Female of *Macrocentrus ancylivora*.
Fig. 4. Female of *Macrocentrus delicatus*.

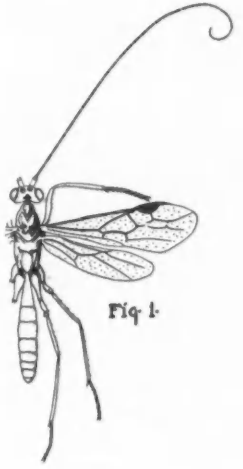


Fig. 1.

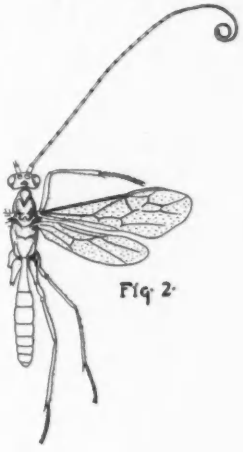


Fig. 2.

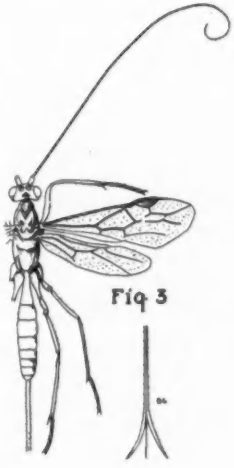


Fig. 3

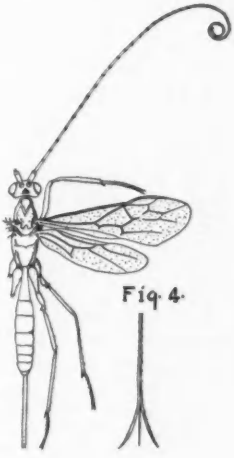


Fig. 4.

THE MAGNOLIA SCALE (NEOLECANIUM CORNUPARVUM THRO.).

GLENN W. HERRICK,
Cornell University.

It is always of great interest to watch the "ups and downs" of insects—to observe the enormous abundance of a certain species over a period of years and then note the gradual subsidence of the species through the following years. For instance, it has actually been difficult during the last few years to find enough fresh specimens of the San Jose Scale about Ithaca for study in the laboratory and for observance in the field. On the other hand the magnolia scale (*N. cornuparvum*) has apparently been increasing in numbers during recent years. My attention has been called, by correspondents, to excessive infestations of the scale followed by serious injury to its host plants, *Magnolia liliflora* and *Magnolia soulangeana*. The scale has been especially prominent in the city of Ithaca and its outlying districts. Undoubtedly the magnolia shrub is becoming more popular as an ornamental and is therefore more commonly planted. Thus the scale has found its host plentiful and readily accessible.

Again, the natural enemies of the scale may have been scarce during the last few years in which event the insect has probably had little to retard its abnormal increase. I have not seen any evidence of parasites working on this coccid and have not been fortunate enough to rear any parasitic forms from the scale.

HISTORY AND DESCRIPTION.

This magnolia scale existed undescribed until 1902. It had been known previous to that time but had been looked upon and discussed as the species, *Lecanium magnoliarum*. In 1903 it was recognized as a distinct species and described by Thro. as *Lecanium cornuparvum* but was later placed in the genus *Neolecanium* (Fernald 1903 and Sanders 1909).

The female scales, the only ones known to exist, for the males have not been observed, are among the largest and most conspicuous of our scale insects, (Pl. I, Fig. 4).

The females, when grown, become about ½ of an inch in length (8-10 mm.). The body is notably convex and is covered with an abundance of white waxy bloom. When numerous, the host plant looks as though it were covered with masses of white cottony material. When the waxy bloom is removed the body of the scale appears shining brown with numerous honey-comb-like pits and large glands. On removal of the body from the branch, an elliptical scar is left on the bark with four distinct, white lines converging toward the center. These lines mark the position of the spiracular grooves of the insect. The legs are short and stubby and the antennæ have but six, short, indistinct segments.

The overwintering nymphs (Pl. I., Fig. 3) are nearly black with a bluish waxy bloom. They are elliptical in outline and somewhat narrower behind. The median carina is high and prominent and slightly lighter in color than the remainder of the body. From 8 to 9 transverse carinæ are present on each side of the median ridge. On each edge of the body are two white spots indicating the entrance to the spiracular grooves. The nymphs vary from .96 to 1.01 mm. in length and from .62 to .76 mm. in width.

The first instar nymph has long, five-segmented antennæ and long slender legs ending in a distinct claw (Pl. I, Fig. 1). The second instar nymph has short, stubby antennæ and legs (Pl. I, Fig. 2). There are three short, stout, spiracular setæ.

FOOD PLANTS AND DISTRIBUTION.

Thro made his original description of the species from specimens taken from Magnolia at Trumansburg, New York. Sanders says it occurs on various species of magnolia including the deciduous *M. acuminata* of the Northern States. Dietz and Morrison (1916) collected it once in Indiana. Houser (1918) records the scale from several places in Ohio on Magnolia and says it has been reported from Daphne and Virginia Creeper, but these two records in all probability refer to *L. magnoliarum*. We have it here in Ithaca on *M. liliflora* and *M. soulangeana*. Pettit and McDaniel (1920) record it from the cucumber-tree at Orwell, Ohio. Dr. Harold Morrison of the U. S. Bur. Ent. very kindly gave me a list of the States from which the scale has been collected according to the records of the Bureau which run as follows:

State	No. of Records	State	No. of Records
Alabama	1	Mississippi	3
Connecticut	1	New York	5
Florida	2	Ohio	10
Georgia	1	Pennsylvania	33
Indiana	1	Virginia	1
Kentucky	1	South Carolina	1
Louisiana	7	West Virginia	6
Maryland	1		

LIFE HISTORY

The insect hibernates as small first stage nymphs on the newer wood. The number of overwintering nymphs is often very great and every available space on the bark is taken up. The nymphs molt rather early in the spring—during the second week in May in 1929. In the first half of June they molt again when each one assumes the elliptical, thickened convex form of the adult. At this time the nymph is of a dark slate, almost purplish color and from 2¼ to 2¾ mm. in length. In about a week each nymph excretes the white layer of wax over the body and each one soon looks like a small snow-white lump of dough clinging to the bark. The nymphs grow slowly during July but by early August a few females may be found which are mature and have brought forth their first young. For instance, on August 2, during the season of 1929, out of several females examined one had 12 nymphs beneath the body (the females are viviparous). This female had matured early for the other four examined were not yet full grown and had no young. By the latter part of August the majority of the females had matured and had brought forth their young, many of which had already settled on the branches. Some, however, on this late date had only begun to bear young which were still beneath the body of the mother scale. There is thus but one generation a year here at Ithaca.

LITERATURE CITED.

Thro, Wm. C. Distinctive characteristics of the species of the genus Lecanium. Cornell University Agr. Expt. Sta. Bull. 209, p. 216, 1903.

Fernald, M. E. Catalogue of the Coccidae. Mass. Agr. Expt. Sta. Spec. Bull. 88, p. 176, 1903.

Sanders, J. C. The identity and synonymy of some of our soft scale insects. **In** Jour. Ec. Ent., Vol. 2, p. 448, 1909.

Dietz, Harry F. and **Morrison, Harold.** **In** the Coccidae or Scale Insects of Indiana, p. 247, 1916.

Houser, J. E. The Magnolia Scale. **In** Bull. 332, Ohio Agri. Expt. Sta., p. 302, 1918.

Pettit, R. H. and **McDaniel, Eugenia.** **In** the Lecania of Michigan. Mich. Agri. Expt. Sta., Tech. Bull. 48, 1920.

Wilson, C. E. **In** Scale Insects of Florida. The Quarterly Bulletin of the State Plant Board of Florida, Vol. VII, No. 4 (July), p. 265, 1923.

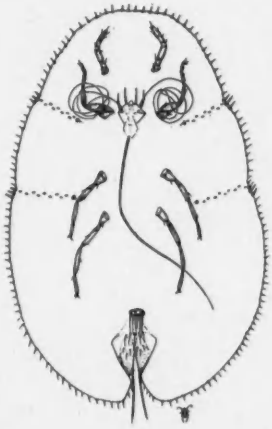


FIG. 1
First stage of magnolia scale.

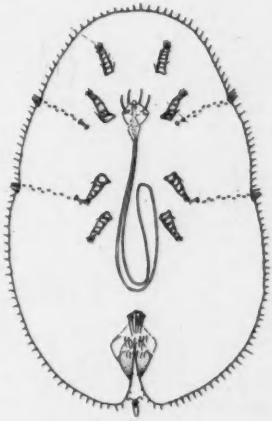


FIG. 2
Second stage of magnolia scale.

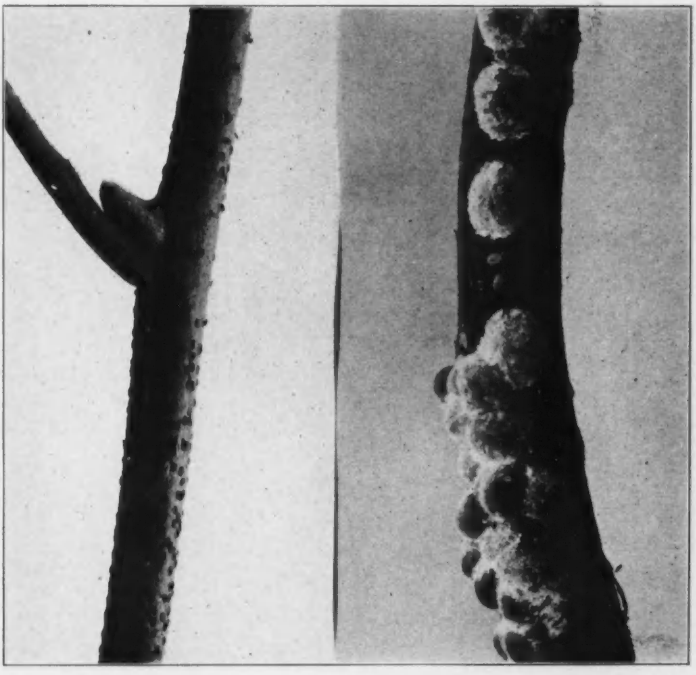


FIG. 3
Overwintering nymphs of the magnolia scale.

FIG. 4
Adults of the magnolia scale. (Natural size.)

INSECTS FROM THE MIOCENE (LATAH) OF WASHINGTON

1. INTRODUCTION, by F. M. CARPENTER
2. HYMENOPTERA AND HEMIPTERA, by T. D. A. COCKERELL
3. ODONATA, by C. H. KENNEDY
4. ISOPTERA, by THOMAS SNYDER
5. COLEOPTERA, by H. F. WICKHAM
6. TRICHOPTERA, by F. M. CARPENTER

I. INTRODUCTION.

F. M. CARPENTER,
Museum of Comparative Zoology,
Cambridge, Massachusetts.

In 1923 C. O. Fernquist, while collecting fossil plants at an exposure of the Latah formation near Spokane, Washington, found three large beetle elytra in the beds. These were the first remains of insects discovered in that stratum and were described by Professor T. D. A. Cockerell* as representing a single species, *Calosoma fernquisti*. No other fossil insects were obtained in the formation until four years later, when Messrs. T. A. Bonser, C. O. Fernquist and E. E. Alexander collected a large number of plants and 33 insects in the vicinity of Spokane. The following year also a few other insects were secured, making a total of 41 specimens. Professor Edward W. Berry, of Johns Hopkins University, in whose hands this collection was placed, turned the insects over to me for identification; but in order to have the affinities of the fossils determined as accurately as possible, I referred most of them to other entomologists, who prepared descriptions of the species belonging to the groups in which they have been interested. For convenience, these several descriptions are being published under the same general title.

It is always interesting, and frequently important, to compare the flora with the fauna of a formation, whenever the two are sufficiently well known. The plants of the Latah beds

*Proc. U. S. Nat. Mus., 1924, *64*, art. 13, p. 4.

were at first described by F. H. Knowlton* in 1923, and they have been more recently and completely revised by Professor Berry†. The latter has recognized 152 species, most of which, of course, are Spermatophytes, although a few Bryophytes, Diatoms, Lycopods, ferns, and conifers are also present. From his study Berry concluded that the Latah flora is an overwhelmingly temperate one, "entirely appropriate to the latitude where it is found and indicative of an ample, well-distributed rain-fall of possibly between 30 and 40 inches annually. It is rather closely paralleled among existing floras by those of such a Middle Atlantic State as Maryland." Berry also substantiated Knowlton's conclusion that the formation is of Upper Miocene age, about the same as the Florissant Shales, Colorado. Knowlton attempted to formulate a picture of the environment of the lake at the time when the plants and insects were entombed: "The area was a broad valley flanked by rolling hills and ridges, some of which rose 1,500 feet or more above the general level, with considerable streams coming down from the north or northwest. Then came the lava flow, which completely dammed the streams, throwing the water back into shallow lakes or ponds . . . . . The open bodies of water were teeming with microscopic diatomaceous life. Here and there pond weeds floated on the surface, and about the borders were patches of cattails, grasses and sedges."

Of the 41 insects that were collected, nine are sufficiently well-preserved for description and accurate determination of their affinities. The other specimens are so badly distorted or macerated that a classification of them would be very vague at best. The described insects belong to several orders: Hymenoptera, Hemiptera, Odonata, Isoptera, Coleoptera, and Trichoptera. Among the more poorly preserved specimens which are not being described, I fail to recognize any additional orders‡, but there is certainly one other family, the Formicidæ. This group is represented by nine specimens, but only one shows much of the body and, as I have already demonstrated§, it is impossible to determine the generic or even subfamily position of an ant by the venation alone, except in a very few

*U. S. Geol. Surv., Prof. Paper, 1923, 140, pp. 1–81.

†U. S. Geol. Surv., Prof. Paper, 1929, 154-H, pp. 225–265.

‡Two dipterous wings have been sent to A. L. Melander, but descriptions have not yet been received.

§The Fossil Ants of North America. Bull. Mus. Comp. Zool., 1930, *70*, No. 1.

cases. The single ant which has the body parts preserved is unfortunately a male, so that it is not possible to determine its affinities either. A photograph of this specimen is reproduced on Plate I, Figure 8.

II. HYMENOPTERA AND HEMIPTERA.

T. D. A. Cockerell,
University of Colorado.

Hymenoptera, Family Apidæ.

I am greatly indebted to Dr. F. M. Carpenter for sending me for description a very remarkable bee, found by Mr. Fernquist in the now famous Latah beds in the State of Washington. To my astonishment, it is a perfectly typical *Bombus*, and as we have no *Bombus* among the numerous fossil bees from Florissant, it suggests that the Latah formation may be younger than the Florissant Shales. I believe it is the first genuine fossil *Bombus* to be described. The so-called *Bombus* from the Baltic amber belong to other genera. *Bombus grandaevus* Heer from Radoboj is not well enough preserved to be placed generically; it is only about 11 mm. long. *B. conservatus* Weyenbergh, from the Jurassic of Solenhofen, is wholly obscure, and there is no reason for regarding it as a bee. *B. jurinei* Heer, from Baden, is a *Xylocopa*, as I ascertained from a study of the type. *B. abavus* Heer I also regard as a *Xylocopa*. *B. crassipes* Novak, from the Aquitanian of Bohemia, and *B. antiquus* Heyden, from Rott, I cannot at present discuss; it is very desirable that the types should be re-examined.

Bombus proavus sp. nov.
(Plate I, Fig. 7.)

♀ (apparently). Head and thorax black, very robust; no exact details can be made out except that there are many long black hairs on the face, as in *B. americanorum*. Anterior wing very well preserved, 15 mm. long; base to stigma, 8 mm.; length of marginal cell, 4 mm.; combined cubitals, on lower side, 4 mm.; basal nervure going a little basad of nervulus; first intercubitus not at all angulate; first cubital on first discoidal slightly longer than second cubital on same cell; second cubital on margin very little more than third on same cell; lower side of third cubital conspiculously bent at insertion of second recurrent. The wing is hyaline, slightly brownish, the upper part of the marginal cell moderately infuscated.

On comparing the wing with those of various species, it seems to come nearest to the European *B. lapidarius* L. (subg. *Lapidariobombus* Vogt.). This species has the first recurrent near upper end rounded, not angled, basal corner of second cubital cell very acute and first intercubitus not bent near lower end, and in almost every respect closely resembles *B. proavus*.

The following salient characters may be used for purposes of comparison:

1. Shape of third cubital cell. In *B. fervidus* Fb. much shorter in proportion to height; in *B. californicus* Sm. quite different; in *B. argillaceus* Scop. third cubital high and short; *B. terrestris* L. has shorter and higher third cubital; *B. mesomelas* Gerst. has much shorter and higher third cubital. The fossil *Calyptapis* from Florissant has the third cubital very long, so there is some reason to think that its shortening is a progressive or modern feature.

2. Angulation of cubital nervure (in sense of Cresson) at insertion of second recurrent. In *B. proavus* the angulation or bending is strongly marked; so also in *Calyptapis*. It is less strongly bent in *B. kirbyellus* Curtis. In *B. cullumanus* Kirby and *B. rufocinctus* Cress. it is little bent. One would suppose the straight vein to be more primitive, but the angulation is especially marked in the fossils.

3. Relative lengths of the upper sides (on marginal cell) of second and third cubitals. In *B. proavus* the second in very little more than third. In *B. fervidus* Fb. it is as much longer than third; in *B. californicus* Sm. the second is about twice as long as third on marginal; in *B. gerstaeckeri* Mor. the second is much more than third; in *B. pratorum* L. second is much longer than third; in *B. ignitus* Sm. the third is strongly bent near the lower end, making this an aberrant species in respect to venation. In *B. incertus* Mor. the second is conspicuously longer than third on marginal; the same is true of *B. eximius* Sm. I take it that the primitive condition is that of the subequal cells.

4. Angulation of first recurrent near upper end. In *B. proavus* the recurrent is gently rounded, not angulate, which I suppose to be the primitive condition. In *B. lapidarius* L. it is rounded. In the following and many others, it is angulate; *B. impatiens* Cress. (with a little projecting point); *B. kirbyellus*

Curt. (no projecting point); *B. vagans* Sm. (angle very strong); *B. argillaceus* Scop.; *B. terrestris* L.; *B. mesomelas* Gerst.; *B. channicus* Grib; *B. cullumanus* Kirby; *B. rufocinctus* Cress. In *Calyptapis* the first recurrent is gently curved, not bent.

5. Relation of lower end of basal nervure to nervulus. In *B. proavus* it goes a short distance basad of it, as in typical *Bombus* and *Psithyrus*. In the typical members of Robertson's sub-genus *Bombias*, and in *B. rufofasciatus* Sm. it meets the nervulus. In *B. rufocinctus* Cress., which Franklin puts in *Bombias*, it goes basad about as in typical *Bombus;* and in *B. cullumanus* Kirby, it goes far basad. It may be that the meeting of the basal and nervulus is more primitive, as they meet in *Calyptapis*, and in the genera of Prussian amber more or less related to *Bombus*.

In *B. americanorum* Fb. the inner angle of second cubital is not so acute as in the fossil. In *B. occidentalis* Greene I found the outer intercubitus bulging much more in the middle (but in a male, this was not so); *B. dahlbomii* Guer., the most southern species, has the marginal cell more parallel sided (less evidently tapering), and second recurrent more remote from end of third cubital cell.

B. proavus is the first fossil bee in the western Hemisphere elsewhere than at Florissant.

Holotype: Museum of Comparative Zoology, No. 2940 ab.

Hemiptera, Family Pentatomidæ (Subfam. Tessaratominæ).

Scudder, in describing the fossil Pentatomidæ from Florissant, noted that the scutellum in the numerous genera is "remarkably triangular and equiangular and destitute of the apical extension common to living types." It appeared reasonable to suppose that since the Miocene time the Pentatomidæ had undergone a forward evolution, resulting in genera which now occupy North America. However, the still older *Pentatomites acourti* (Ckll.), from the Isle of Wight Oligocene, had the scutellum prolonged apically, with a light spot at the tip, such as may often be seen in modern forms. This follows the interpretation of Mr. W. E. China, who examined the type. Furthermore, there is a living group, the Tessaratominæ, many genera of which have exactly the kind of scutellum described

and figured by Scudder. It includes the largest known Heteroptera, according to Distant, and is well represented in the Oriental, Ethiopian, and Australian regions. In America, it is now greatly reduced in numbers, with a species of *Pantochlora* in Mexico and Guatemala, and two species of *Piezosternum*, one found at Rio de Janeiro, the other spread from Mexico to the West Indies, Columbia, and Guiana to Brazil. It appears probable, with such evidence as we have, that the Tessaratominæ were once the dominant Pentatomidæ in America, but have now been almost entirely replaced by other groups: a shifting comparable to that already demonstrated in the Bombyliidæ.

From the Latah formation at Spokane we now have a very fine species of the same alliance, but not referrable to any of the Florissant genera, though perhaps as near to *Teleoschistus* as to any. There is a rather strong general resemblance to the genus *Origanaus* of Distant from the Naga Hills, India, but that is narrower and has a shorter scutellum.

Latahcoris, gen. nov.

Head (not preserved, but width judged by excavation of pronotum) less than a third as wide as pronotum; pronotum profusely and coarsely punctate, more than twice as wide as long, the lateral margins produced into large obtuse lobes, much as in *Podisus luridus* Fabr.; scutellum triangular, subequilateral, with straight sides and no pronounced apical lobe, its surface coarsely punctate, with an ill-defined impunctate median band (probably it was a pallid line, as in *Amirantea gardineri* Distant); corium broad, unmarked. Appendages not preserved. Longitudinal veins of membrane apparently few.

Genotype: Latahcoris spectatus, new species.

Latahcoris spectatus, sp. nov.

Width of pronotum 12 mm., its length in middle 4.3 mm., but to corners next to eyes, 5 mm.; disc darkened, with three faint pale lines, the outer one gently arched, with the convexity outward. Width of scutellum about 8.5 mm.; length of a side about 8 mm.; length of scutellum, about 6.5 mm.; end of scutellum to end of membrane, about 7 mm.

Holotype: Museum of Comparative Zoology, No. 2941 ab; Brick Yard, Spokane, found in 1927 by E. E. Alexander.

III. ODONATA.

CLARENCE H. KENNEDY,
Ohio State University.

FAMILY LIBELLULIDÆ, SUBFAM. CORDULINÆ.

Miocordulia, gen. nov.

Based upon a right hind wing, probably female. This fossil is well preserved, but was apparently in a worn and fragmentary condition when embedded.

Five antenodals, ten postnodals; five crossveins in R1 area between subnodus and level of stigma, the next crossvein of this row being the single crossvein below the inner end of the stigma which is not developed as a brace vein. Stigma four times as long as wide. Median space free; the arculus arising midway between the first and second antenodals; M1-3 and M4 arising separately on the arculus near its posterior end. (R-M1-3 area between arculus and subnodus collapsed but probably with three crossveins as occur in most of the related genera.) Two crossveins below subnodus connecting it with the bridge vein, the next or third crossvein of this series being the diagonal crossing of Rs; thirteen simple crossveins between M2 and Rs beyond the Rs crossvein. An Rs supplementary sector about ten cells long. Eighteen crossveins between M3 and M4; a short supplementary sector of four large cells being M4. Three rows of cells between M4 and Cu1. This three-rowed area extends out from the triangle a distance of six cells, ending at the level of the fork of M1-2 and the bridge vein.

Subtriangle present; triangle crossed, its inner angle arising at the lower end of the arculus; Cu-A crossvein midway between triangle and base of wing; fourteen cells between Cu1 and Cu2, cell No. 7 being at apex of the anal loop. (Anal loop with only the base, upper tier of cells and apex of loop preserved.) Nine cells in the upper tier of the loop; three cells across the base of the loop, the third or extra cell being triangular and separating the upper and lower tiers of the loop. On vein A basad of the loop arise three veins which extend into the anal field. The first of these from the base of the wing is heaviest and curves after the fashion of the vein bounding the outer side of the anal membrane, which it probably is though no remains of the membrane are evident. Thus between the inner angle of the subtriangle and the base of the wing are five cells behind vein A*. (Three rows of five to six sided cells in the anal area behind the anal loop?)

The courses of the main wing veins are as follows: M1a well developed, arising under outer end of stigma and divirging from M1;

*The area behind A between the base of the wing and the anal loop is identical with that in the female Epicordulia. In the male this area is more condensed.

M2 and Rs divirging in first third of course then converging to the level of the stigma, then slightly divirging to margin of wing. M3 and M4 slightly converging to level of subnodus, then slightly divirging to outer fourth after which they converge rapidly to the margin of the wing. A mere suggestion of sinuosity in the course of M3.

Genotype: *Miocordulia latipennis* new species.

Miocordulia latipennis, sp. nov.
(Figs. 1, 2; Plate I, Fig. 6.)

Approximately 35 mm. long and 11 mm. broad at the level of the nodus; base to nodus, 14 mm.; stigma, 4 mm. long, by 1 mm. broad. Other characters as given in the generic description.

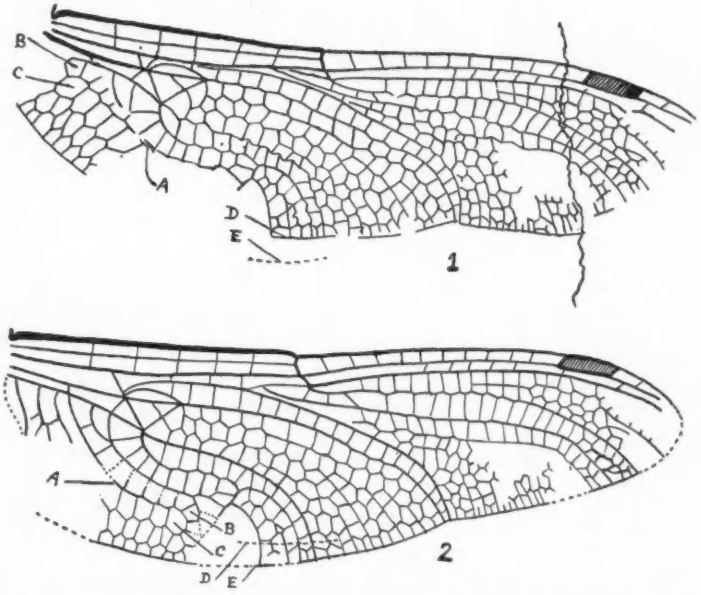


Fig. 1. *Miocordulia latipennis* Kennedy. Drawing of the fossil wing as it appears on the obverse print. The area from A to C is out of place and reversed lengthwise.

Fig. 2. Restoration of the wing of *Miocordulia latipennis* Kennedy.

Holotype: Museum of Comparative Zoology, No. 2942 ab. Found near Spokane, Washington, by Mr. C. O. Fernquist, 1927.

Discussion: Fig. 1 is a drawing of the fossil itself. The tip of the wing, the area below the supplementary sector of Rs and the area below the anal loop are missing.

A curious anal area at the extreme base of the wing is present, an anal area like nothing else in the Cordulines as it extends too far basad by a distance of at least two cells. Just casually it appears to connect up with the anal loop and vein A. This is as it appears on the obverse. From a study of the reverse suspicions arose that this connection was not so certain. Apparently branches of vein A passed under this anal area. The author took the liberty of chipping enough off of the reverse to expose fully these basal veins as shown in Fig. 2. This showed at once that this anal area was a loose fragment entirely out of position. How then to interpret the anal fragment?

An examination of Fig. 1 shows that nowhere unless at the right upper corner of the anal fragment is it absolutely continuous with the main fossil print. Each of the other (apparently connecting) crossveins is broken. As located in Fig. 1 the anal area does not fit any genus of living Cordulinæ. The writer believes that it is a fragment from beneath the outer end of the anal loop which has floated up and over, towards the base of the wing, thus lying under surface up with its ends reversed. Its distal end then lies at the extreme base of the wing and its basal end under the base of the anal loop. If this is true then it should be reversed and its present basal end become its apical end at the anal loop as shown in Fig. 2. The connection (A) in Fig. 1 appears confused in the fossil as though there were a doubling up of crossveins. This is probably the anchor or axis about which the fragment rotated and was probably attached to the third cell of the upper tier of the anal loop.

The whole wing is obviously distorted in minor ways. Fig. 1 shows the many wavy and crumpled crossveins in the disc of the wing. In the restoration, Fig. 2, this area has been widened, the distance from D to E. The fragment on the other hand appears to have been stretched as all of its crossveins are tense and straight. Moreover, its true distal end is too wide to fit within any contour under the outer end of the anal loop. To make the fragment fit under the apex of the anal loop the outer end of the fragment was narrowed to bring its hind edge within the contour of the hind edge of the main

fossil as drawn in the restoration, Figs. 2, E. When this was done every detail of the fragment fitted logically. The cell B, Figs. 1 and 2, is in the turn of the anal loop and the eight-sided cell C falls into its natural place. The vein from A to B becomes natural in that its A-end is heavy and straighter than the B-end which becomes more zig-zag. Thus it forms, with the curve around cell C, the vein bounding the under side of the anal loop. This solution places the vein A–B in a logical position and also takes care of the puzzling cell B which is perfect and complete in the fossil and because of its shape can be fitted nowhere else as precisely.

This gives a wing which has characters of *Somatochlora* and of *Epicordulia* yet differs from either in the three rows of cells extending outward from the triangle and in the greater width of the base. It differs from Somatochlora in having three rows of cells behind the anal loop and from Epicordulia in having a subtriangle. It is also close to Epitheca which has a subtriangle, four rows of cells behind the anal loop and almost three rows of cells beyond the triangle. Thus this fossil has characters of the European *Epitheca*, the American *Epicordulia* and the Holarctic *Somatochlora*. Apparently it is closest to the European *Epitheca* though the shapes of the cells of the anal area of that genus are less regular than those of *Somatochlora* and *Miocordulia*. As *Epicordulia* with a widely spread eastern species, *princeps*, and a Florida species, *regina*, stands apart as a genus from our other American Cordulinæ this genus, *Miocordulia*, may be a link connecting it back to the Palaearctic fauna.

Epicordulia regina is one of several species of Odonata that are rather definitely limited to Florida, a group of species which the writer has felt may date back to the old Miocene island of Florida off the coast of our present Georgia. If *regina* arose by isolation in the Miocene island of Florida, this gives us a slight check on the time of the entry of the *Miocordulia* and *Epicordulia* stock into America from the Orient.

IV. ISOPTERA.

THOS. E. SNYDER,
Bureau of Entomology, U. S. Dept. of Agriculture.

FAMILY RHINOTERMITIDÆ.

The fossil termite which was sent to me for identification proves to be a species of *Stylotermes* new to science. The genus *Stylotermes*, in the family Rhinotermitidæ, was established by Karin and Nils Holmgren in 1917, (Mem. Dept. Agric. India, vol. 5, No. 3, p. 141-2), with an East Indian species as genotype. This termite from South India is the only *living* representative of this genus. However, at least one *fossil* species occurs in Baltic Sea amber. *Stylotermes* is of particular interest since it exhibits characters which are connecting links between the lower termites in the family Kalotermitidæ and those in the intermediate family Rhinotermitidæ.

Stylotermes washingtonensis n. sp.
(Plate I, Fig. 5.)

Wing. Forewing (?). Subcostal vein joined to the costal margin by numerous vertical short veinlets. Wing membrane strongly reticulated with accessory veins arising vertically from the nervures. Median vein free from stump, closer to cubitus than to subcosta with numerous, (as many as 20), closely placed, branching branchlets to posterior margin of the wing. All veins are prominent and thickened. Wing scale or stump not present.

Length of wing: 11.5 mm.
Width of wing at widest portion: 3.0 mm.

Holotype: Museum of Comparative Zoology, No. 2943 ab. Collected by C. O. Fernquist, near Spokane, Washington.

V. COLEOPTERA.

H. F. WICKHAM,
University of Iowa.

Two specimens are in such fragmentary or imperfect preservation as to give no particular clue to their position, but the remainder fall into two species which appear to be readily placed. Descriptions of the latter follow.

FAMILY CARABIDÆ.

Pterostichus fernquisti n. sp.

(Plate I, Fig. 1.)

Represented by three elytra, one in obverse, the other two in reverse. Form only moderately elongate, striæ fine, not very deep, minutely punctured. Scutellar stria of moderate length, joining the sutural. Interspaces very little convex. Marginal interruption strong. Ocellate submarginal punctures strong, rounded, close together behind the humerus, then widely spaced, becoming deeper and closer again on about the apical half.

Length, 11 mm.; greatest width, 3.50 mm.; length of scutellar stria about 1.75 mm.

This seems to be a genuine *Pterostichus* of the same general type as the numerous recent species inhabiting the Pacific coast of North America and extending into the Rocky Mountains. Perhaps it is most reminiscent of *P. gracilior.*

Holotype: Museum of Comparative Zoology, No. 2944 ab; paratypes, Nos. 2945, 2946. Holotype, an obverse. Paratypes, two specimens in reverse, labelled Deep Creek Canyon, C. O. Fernquist, 1928.

FAMILY DYTISCIDÆ.

Dytiscus latahensis n. sp.

(Plate I, Fig. 3.)

Represented by somewhat less than the distal half of a left elytron which, by its tapered form, evidently belonged to a species not decidedly broader behind. The surface shows the posterior ends of five impunctured sulci and the barely visible tips of two others, all shallow for the short distance over which they are impressed. Posterior to these, the elytron is finely punctured, becoming more heavily so apically, but none of this punctuation is so pronounced as in our recent *D. fasciventris.* The sutural stria is fine visibly punctate and traceable nearly to the apex. The outer elytral edge is marked by a light submarginal stripe, giving off, near its tip, a broader arcuate curved band with the convex side anterior.

Length of fragment, along suture, 10.8 mm.; width 8.70 mm.

Not unlike the figure of *D. lavateri* Heer, from the Oeningen beds, but that does not exhibit such a long sutural stria. This stria is also less plainly marked apically in all of the recent species to which I have access, the nearest approach to it being in some specimens of *D. harrisi.* The markings described appear to be a genuine elytral pattern and not due to abrasion. From the presence of sulcations it is presumed that the specimen was a female.

Holotype: Museum of Comparative Zoology, No. 2947. Marked E. E. Alexander, Spokane, Washington, 1927.

VI. TRICHOPTERA.

F. M. Carpenter,
Harvard University.

Six specimens of caddis-flies as well as caddis cases* are present in the collection of Latah fossils. Considering their aquatic development, it is not surprising that these insects should be represented, but the number of species is much larger than one would expect in a collection of this size. Fifteen per cent of all the specimens belong here. The magnitude of this proportion takes on some significance when we compare the trichopterous fauna of the Latah beds with that of the Florissant Shales, Scudder's examination of about twenty thousand Florissant insects showed that less than 4% of the species were Trichoptera, which means that the caddis-flies seem to be about four times as numerous at the Latah beds as at those of Florissant. It is also interesting to note that of the six Latah specimens, five are Limnephilids (representing five species) and the other is a *Phryganea*. In marked contrast to this, the specimens in the Florissant Shales comprise 95% Hydropsychids, 4% Phryganeids, and 1% Limnephilids. In other words, the family Hydropsychidæ, which is far and away the most abundant at Florissant, is absent in the Latah collection, while the family Limnephilidæ, of which only two species have been found in some twenty thousand Florissant insects, is represented by five species out of a total of 41 fossils from the Washington deposit. It must be admitted, of course, that these statements lose some of their force in view of the small number of Latah insects known, but I nevertheless believe that they have considerable significance. The Hydropsychidæ, which are so abundant at Florissant, breed only in rapid streams or active waters of lakes. The Phryganeidæ and very nearly all the Limnephilidæ, on the other hand, develop in standing water which usually contains much plant life, or in quiet streams. This would seem to verify Knowlton's conclusion, quoted above, that the lake which deposited the beds was shallow and contained a diverse flora.

*Berry, Edward W. A Caddis Case of Leaf Pieces from the Miocene of Washington. Wash. Acad. Sci. Jour., Vol. 18, No. 3, pp. 60–61, Fig. 1, (1928).

FAMILY PHRYGANEIDÆ.

Phryganea spokanensis sp. nov.
(Fig. 3.)

Described from a well-preserved fore wing, complete except for the very apical margin. Length, 19 mm.; width, 5 mm.; anterior margin slightly convex, apex regularly rounded, posterior margin gently curved; subcostal space broad, much as in the recent *Ph. varia;* Sc quite straight; R1 close to Sc, straight, with a prominent pterostigmal hump; discoidal cell slender; Cu diverging from M well beyond the origin of Rs; the common stem Cu+M joins R at the base of the wing; M3+4 unbranched; 1A and 2A close together at base; 3A looped to 2A distally, and 4A looped to 3A, as characteristic of the genus.

Holotype: Museum of Comparative Zoology, No. 2948.

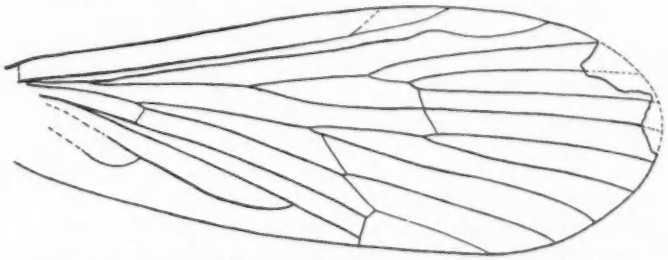


Fig. 3. *Phryganea spokanensis* Carpenter. Drawing of fore wing.

The generic characteristics of this fossil are so obvious that I do not hesitate to place the species in the genus *Phryganea*. The looping of A3 and A4 distally; the shape of the discoidal cell, with a large part of R2 forming a portion of the anterior wall; and the shape of the thyrid cell, with its oblique distal wall, are characters not found combined in any other genus. *Phryganea* is represented by nearly 30 extant species, widely distributed in Europe, Asia, North America, and portions of South America.

FAMILY LIMNEPHILIDÆ.

Miopsyche, gen. nov.

Allied to *Limnephilus*. Anterior margin convex; apical border flattened, as in *Limnephilus;* posterior margin straight or slightly concaved; pterostigma distinct; discoidal cell long; anal veins as in *Limnephilus*.

Genotype: Miopsyche alexanderi, sp. nov.

The genera of Limnephilidæ, of which there are about fifty described, present a diversified wing structure, so diverse, in fact, that it is impossible to determine from wing characters alone the exact position of a species. Rather than attempt to assign these two Latah Limnephilids to a recent genus, I establish a new one for their reception until other specimens are found showing sufficient body characters to enable us to determine more accurately the generic affinities.

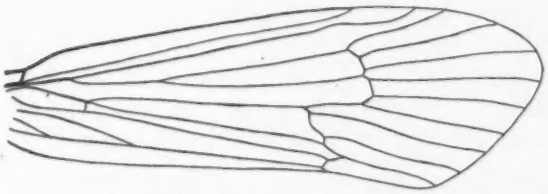


Fig. 4. *Miopsyche alexanderi* Carpenter. Drawing of fore wing.

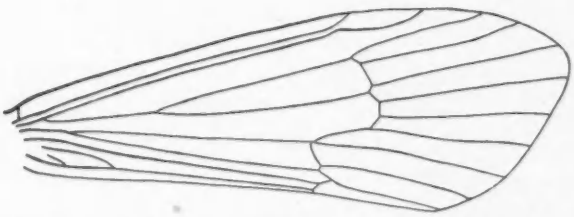


Fig. 5. *Miopsyche martynovi* Carpenter. Drawing of fore wing.

Miopsyche alexanderi, sp. nov.
(Fig. 4.)

Described from a complete fore wing. Length, 20.0 mm.; width, 6.0 mm. Subcostal space broad, much narrowed basally. R1 straight up to the pterostigmal hump; basal walls of first and second apical cells equal; subradial cell only slightly broader apically than basally; basal walls of sixth and eighth apical cells equal; that of the seventh cell much longer, and gently sigmoidal.

Holotype: Museum of Comparative Zoology, No. 2949. Collected at Spokane, by E. E. Alexander, for whom the species is named.

Miopsyche martynovi, sp. nov.
(Fig. 5.)

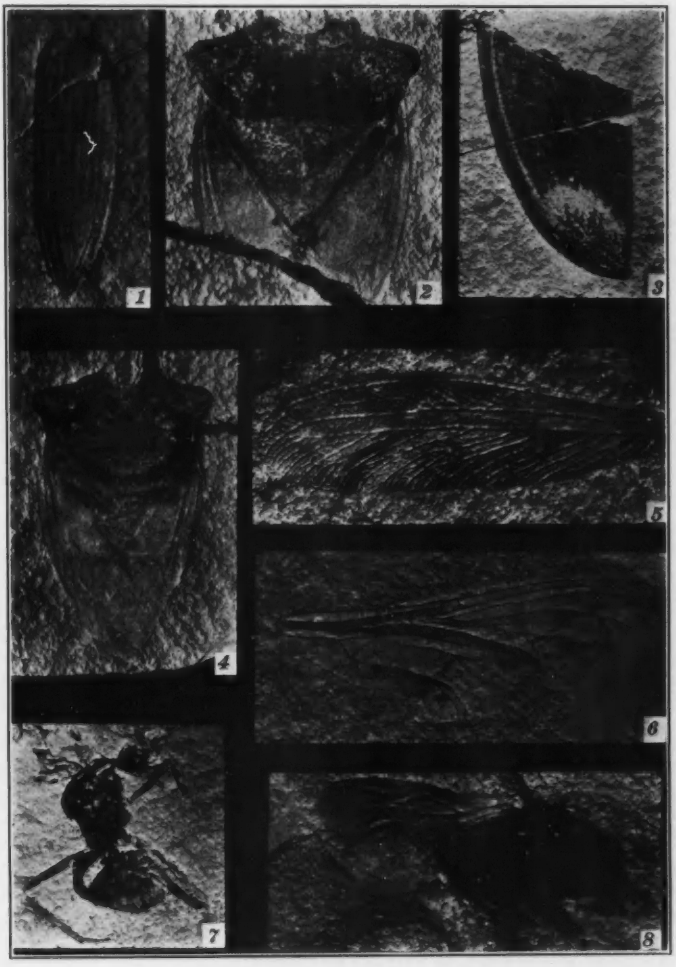
Described from a complete fore wing. Length, 17.0 mm.; width, 5.0 mm. Anterior margin more convex than in preceding species, apical border more rounded, and wing broader apically. Subcostal space much narrower than in *alexanderi;* basal wall of first apical cell about ½ as long as that of the second; discoidal cell narrower than that of foregoing species; subradial cell much broader distally than basally; sixth apical cell pointed basally; basal wall of seventh apical cell about three times as long as that of cell eight.

Holotype: Museum of Comparative Zoology, No. 2950. This species is named for Dr. A. V. Martynov, in recognition of his investigations on Trichoptera and fossil insects.

The other caddis-fly wings in the collection are incomplete, only the distal halves being preserved. It is obvious from their shapes and preserved portions that they represent distinct species, all of the family Limnephilidæ; but because of the absence of the basal parts of the wings, we find it impossible to determine their generic affinities. In view of the abundance of trichopterous wings in the Latah beds, it is very likely indeed that complete specimens of these species will soon be found. Meanwhile, rather than add to the already too long list of fossils with "uncertain" affinities, we shall wait for further material before describing and naming the species.

EXPLANATION OF PLATE.

Fig. 1. *Pterostichus fernquisti* Wickham, holotype, (× 4).
Fig. 2. *Latahcoris spectatus* Cockerell, holotype reverse, (× 3).
Fig. 3. *Dytiscus latahensis* Wickham, holotype (× 4).
Fig. 4. *Latahcoris spectatus* Cockerell, holotype obverse, (× 2.5).
Fig. 5. *Stylotermes washingtonensis* Snyder, holotype (× 5).
Fig. 6. *Miocordulia latipennis* Kennedy, holotype reverse, (× 1.8).
Fig. 7. Male ant, (× 4).
Fig. 8. *Bombus proavus* Cockerell, holotype (× 2).


1
2
3
4
5
6
7
8

ECOLOGY OF TOXOPTERA GRAMINUM, ESPECIALLY AS TO FACTORS AFFECTING IMPORTANCE IN THE NORTHERN UNITED STATES.*

F. M. WADLEY.
Bureau of Entomology, Washington, D. C.

CONTENTS.

PAGE

INTRODUCTION 326
PART I. A study of the ecology of *Toxoptera graminum* 327
Life history in general 327
Effects of temperature 329
Effects on life, reproduction and development 329
Effects on proportion of biological forms 334
Effects of extreme cold 336
Effects of extreme heat 338
Effects of humidity 340
Effects of light 341
Effects of various weather phenomena 345
Rain 345
Snow 346
Wind 346
Food relations 347
Injury 347
Food plant species 348
Reactions to food plants 348
Other factors 352
Appearance of biological forms 354
Winged and wingless females 354
Sexual forms 355
Migrations 356
Potential increase of population 359
Enemies 364
Coccinellids 365
Syrphids 368
Hymenopterous parasites 371
Cecidomyiidæ 372
Chrysopidæ 373
Biological control as a whole in Minnesota 373
PART II. Factors affecting distribution, especially as to northern outbreaks 374
Distribution records 374
Influence of rainfall on distribution 375
Effect of summer conditions 378
Limitations due to winter cold 379
Winter eggs 379
Survival of active aphids 380
Spring or summer migration to northern states 381
Probable sources and spread of 1926 outbreak 386
Probability of northern outbreaks 389
SUMMARY 390
LITERATURE CITED 393

*Published as Paper No. 1003 of the Journal Series of the Minnesota Agricultural Experiment Station.

Introduction.

The unexpected and severe outbreak of *Toxoptera graminum* Rondani, a grain aphid often called the "green bug," in Minnesota in 1926, has led to an investigation of factors governing such outbreaks. Such a study seems desirable because of the light it may throw on its capacity for injury, especially in the north. It is also of interest because of the need for more information on the life economy of the aphid group in general.

Credit is due Dr. R. N. Chapman, Dr. W. C. Cook and Prof. A. G. Ruggles, under whom the work was carried out; and to other members of the Minnesota faculty, and graduate students, for many helpful suggestions. Records of the United States Weather Bureau have been freely used, Mr. Pursell of the Minneapolis office helping to make them available.

Since the original description in 1852, from Italy (Rondani 1852) the species has periodically been injurious and has attracted considerable attention, as evidenced by numerous articles. A large part of this literature is summed up by Webster and Phillips (1912). Some articles have appeared since, the more important from the present standpoint being by Headlee (1914), Moore (1914), Phillips (1915), Kelly (1917), Luginbill and Beyer (1918), Tucker (1918), Walton (1921), Garman (1926), Sanborn, Brown, and Bieberdorf (1926), Ruggles and Wadley (1927), and Wadley (1929). The recorded distribution includes large parts of North America, Europe, Asia and Africa, with the greatest injury in the southern United States, Italy, Hungary, Southern Russia and South Africa. The literature shows that the species is quite similar in its life history to other important aphids, except that the winter egg plays a less important part than with some others. Relations to enemies are like those of other aphids. With unimportant exceptions, only grasses have been recorded as hosts, and wheat and oats as most injured. The species seems to have an unusual power of inflicting injury.

Besides Webster and Phillips' comprehensive bulletin, several papers have dealt especially with ecology. Glenn (1909) worked on relation to climate, Headlee (1914) on effects of moisture and temperature, and Moore (1914), Tucker (1918) and Luginbill and Beyer (1918) discussed ecological problems. In the present work the effort has been to carry on a careful

study of the ecology of the species, and to apply known facts to problems of distribution. Previous contributions will be more fully discussed in treating the subjects to which they apply.

PART I.

A Study of the Ecology of Toxoptera Graminum.

LIFE HISTORY IN GENERAL.

The life cycle agrees in many respects with that typical of the Aphididæ. Winged and wingless females reproducing parthenogenetically and viviparously are the forms usually found. The wingless females occur most abundantly and constantly. Winged females produce progeny nearly all wingless, while wingless parents produce both winged and wingless progeny. Under certain conditions, typically in the fall, the parthenogenetic families may include some winged males, and wingless non-parthenogenetic oviparous females. The eggs produced by the latter after mating may pass the winter, and hatch in the spring, producing wingless parthenogenetic females. These types of adults may be termed biological forms. Males, oviparous females, and eggs, appear to be rare in the field in Minnesota; and are probably not of much significance in the economic importance of the species. The males and oviparous females are usually referred to as "the sexes" or "sexual forms" to distinguish them from the parthenogenetically reproducing winged or wingless females, and a variety of other terms for them occur in the literature. The writer prefers the term zygogenetic, used by Wilson (1915) to distinguish them from the parthenogenetic forms, although usage makes the simpler term convenient.

Detailed life history studies are reported by several workers, especially Washburn (1908, A, B, C), Hunter (1909), and Webster and Phillips (1912). They include figures, descriptions and measurements. Washburn's work is of special interest because it was done in Minnesota, and includes the first description of males and oviparous females.

The species may be distinguished from other grain aphids by the once-branched media in the winged form; also by the pea-green color with darker green dorsal line, the black eyes, and the green cornicles with dark tips. The wingless parthenogenetic female is typically about 1.8 mm. in length and .8 to .9 mm. in greatest width. The winged female is somewhat smaller, the oviparous female a little larger, and the male smallest of all. Unfavorable conditions have produced smaller adults.

The nymphs pass through four instars in development, the time required being about a week with summer temperature, but varying widely. Advanced embryos occur in late fourth instar nymphs. The wingless parthenogenetic females may begin reproduction within a few hours after the last molt; winged females usually do not reproduce

until 24 to 48 hours after the molt. In Table I are assembled rearing records, secured in chimney cages on oat plants, in the greenhouse from April 1 to September 30, and in the outdoor insectary in June, July and August. In these cases food, temperature and day-length were all fairly favorable.

TABLE I.

ADULT LIFE AND REPRODUCTION UNDER FAVORABLE CONDITIONS.

	WINGLESS PARENT			WINGED PARENT		
	No.Cases	Average	Range	No.Cases	Average	Range
Total number young..	19	63.1	2 to 83*	4	39.5	14 to 51
Days of reproductive period.....	19	22.7	1 to 37	4	16.8	6 to 23
Days post-reproductive life.....	19	2.7	0 to 9	4	5.0	1 to 10

*Only one case less than 40.

TABLE II.

OUTDOOR REARING RECORDS BY MONTHS.

Month	Approximate No. Generations Reared	Young per Day; Wingless Parents Early in Reproduction*	Average Temperature ° F.
1926.			
August.....	3½	3.7	70.5
September.....	2 +	2.5	57.5
October.....	1 +	0.8	48.5
1927.			
April.....	½	0.6	48.0
May.....	1½	1.0	55.0
June.....	3	2.3	64.0
July.....	4	3.0	71.0
August.....	3	2.6	67.5
September.....	2 +	...	64.0
October.....	1 +	1.4	53.5

*First 10 days.

Reproduction rate early in adult life is of more importance in rapid increase than the rate throughout life. An average of 3.5 young per day for the first 10 days of reproduction, was secured from 31 wingless females, kept under rather favorable conditions, in insectary and greenhouse. Four young per day seems to be about the maximum rate which can be sustained several days by young wingless adults, although as many as 10 have been produced in individual days. Winged adults are less prolific.

Oviparous females produced an average of about three eggs each and a maximum of seven in this study; usually not more than one in a day. They did not oviposit sooner than 3 to 5 days after maturity and not later than 15 days, though some lived nearly a month as adults. Eggs failed to darken normally when males were not kept with the females, and in some cases when they were. Webster and Phillips (1912) discuss the embryology of these eggs, and note that they will not hatch unless they have been subjected to freezing weather.

EFFECTS OF TEMPERATURE.

The effects of temperature include effects of variations within the range of possible development, and of extreme temperatures.

The effects of temperature within the range of development may be observed in rate of development, rate of reproduction, total length of life and number of young, and appearance of biological forms. Population increase is a resultant of some of these factors.

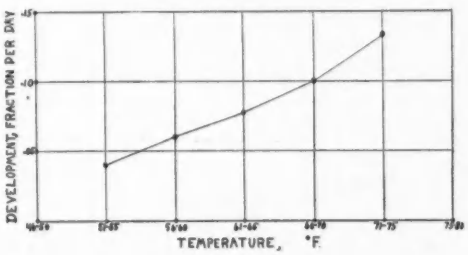


Fig. 1. Temperature and rate of development, outdoor results. By five-degree groups.

Effects on Life, Reproduction and Development.

Rearing records in the outdoor insectary are summarized in Table II, and data on development are graphically presented in Fig. 1. Rearing was done in chimney cages on oats, using wingless parents except in one case (June 21). A maximum and minimum thermometer set was used except in August and September, 1926, when a Tycos recording thermometer was used, and in May and June, 1927, when St. Paul Weather Bureau records were used. Insectary temperatures were near those recorded by the Weather Bureau throughout the work.

In both 1926 and 1927, slow development took place in October, but none in November. The aphids perished from cold during the latter month. In 1927, March was too cold for reproduction, only 5 days averaging above 44° F.; a parent was caged outdoors on April 4, and first reproduced April 11.

Summer temperatures in Minnesota were usually a little too low for maximum growth and reproduction. Rearing at outdoor temperatures has been recorded by Webster and Phillips (1912) for Indiana and

northern Texas; by Tucker (1918) for northern Texas; and by Luginbill and Beyer (1918) for South Carolina. In Indiana, in summer months averaging about 75° F., reproduction appears to be as rapid as in late spring or early fall, and development more rapid. In Texas and South Carolina, where summer months average 80° F. or higher, reproduction is depressed by the heat, but development is nearly as rapid as in May and September.

TABLE III.

DATA ON DEVELOPMENT.

	Temperature ° C.	° F.	No. Reared	Average Days to Develop	Range, Days
Wingless	7	44.6	4	33.2 ± 1.078	30 to 36
	10	50.0	44	31.8 ± .257	26 to 37
	12	53.6	21	20.8 ± .307	19 to 27
	14	57.2	49	17.9 ± .150	14 to 22
	17½	63.5	53	11.6 ± .091	9 to 14
	20	68.0	51	8.4 ± .072	7 to 10
	22–23	72.5	61	7.2 ± .059	6 to 9
	26	78.8	31	6.5 ± .082	5 to 7
	30	86.0	71	5.9 ± .061	5 to 8
	32	89.6	17	6.9 ± .306	6 to 14
	33	91.4	2	7.0	No range
Winged	10	50.0	4	34.5 ± 1.118	31 to 39
	12	53.6	16	26.1 ± .313	24 to 31
	14	57.2	12	19.4 ± .232	17 to 21
	17½	63.5	7	13.0	None
	20	68.0	11	9.0 ± .091	8 to 10
	22–23	72.5	16	7.6 ± .106	7 to 9
	26	78.8	19	6.4 ± .073	6 to 7
	30	86.0	12	5.5 ± .102	5 to 6
	32	89.6	6	6.0 ± .269	5 to 7
Males	17	62.6	5	11.9	11 to 14
	22	71.6	4	7.7	7 to 9
Oviparous Females	17	62.6	2	12.5	12 to 13
	22	71.6	2	7.5	7 to 8

Laboratory results are more exact and satisfactory in a study of temperature effects. Headlee (1914) records results with constant temperatures of 50°, 60°, 70°, 80°, and 90° F., finding reproduction and development most rapid at 80°. In the present work rearing was done in chambers regulated by thermostats controlling heating lights; those below room temperatures were cooled by ammonia-chilled brine in the back walls. Temperatures were practically constant. Constant light was supplied by 100-watt nitrogen "daylight" bulbs shining through the glass ceilings and concentrated by shades; small electric fans kept the air in motion. Lamp chimney pot cages containing oats were used. Humidity was not measured; other experiments

showed that Toxoptera thrives in a wide range of humidity. The plants did not hold up as well as in the greenhouse, probably because of the smaller amount of light. However, rearing was carried on without difficulty. Data are believed to show the effect of temperature quite accurately, and results in the different chambers are strictly comparable with each other.

TABLE IV.

REPRODUCTION AND ADULT LIFE.

Temperature		No. Adults Used	Average Young per Day		Average Total No. Young	Mean Reproduction Period, Days	Mean Adult Life, Days
			Early in Period	Whole Period			
° C.	° F.						
			WINGLESS ADULTS				
7	44.6	2	0.41	0.41	7.5	18.5	22.0
12	53.6	6	1.0	0.88	25.0	28.5	31.2
17–17½	63.0	8	2.19	1.84	37.1	20.1	20.8
20	68.0	4	3.06	2.28	52.5	23.0	24.0
22–23	72.5	8	4.32	3.71	52.1	14.0	14.3
*26–27	79.7	6	4.09	3.58	69.3	19.3	20.3
30	86.0	4	3.74	2.77	36.8	13.3	14.0
32	89.6	7	1.72	1.72	7.9	4.6	6.9
34–35	94.1	3	1.75	1.75	4.7	2.7	6.0
			WINGED ADULTS				
7	44.6	2	0.37	0.37	10.0	27.0	41.0
12	53.6	2	0.66	0.66	10.5	16.0	21.5
17½	63.5	3	1.48	1.28	19.7	15.3	17.7
†20 (all long lived)	68.0	6	2.03	1.72	19.5	11.3	13.2
20	68.0	3	2.29	1.78	35.0	19.7	21.7
23	73.4	3	2.48	2.52	43.0	17.3	18.3
26	78.8	3	2.25	2.36	34.7	14.7	17.0
30	86.0	3	2.0	1.73	17.3	10.0	13.3
32	89.6	4	1.8	1.8	8.5	4.8	9.8
34–35	94.1	2	1.0	1.0	4.0	4.0	8.0

*At 26–27°C., 3 wingless adults escaped before completing their reproduction period.

†At 20°, 3 alate adults died soon after maturity for some unknown reason; hence 3 others were used and averaged with the first 3.

In the work on development, several parents from the greenhouse were caged together and allowed to produce a number of young of the same age, then removed. The cage was then put in the desired temperature chamber, the young reared, and removed each day, as they matured. Periods for individual aphids were recorded in days, without fractions. A majority of the nymphs started usually matured; however, at 7° and 32° C., considerably less than half were reared successfully.

The probable error of the differences between times of development at any two temperatures, is the square root of the sum of the squares of their probable errors. In most cases this error is very small in proportion to the difference, indicating that the difference is significant. Exceptions are found at the extremes of the series, where only a few were reared.

In work on adult life and reproduction, large nymphs from the greenhouse were caged at constant temperatures until death, progeny being counted and removed daily. The daily average number of young early in adult life has been computed, as before, as a good index to rapidity of increase. The period used here is the time previous to maturity of oldest offspring at the given temperature. At low and high temperatures this is no shorter than the entire reproductive period.

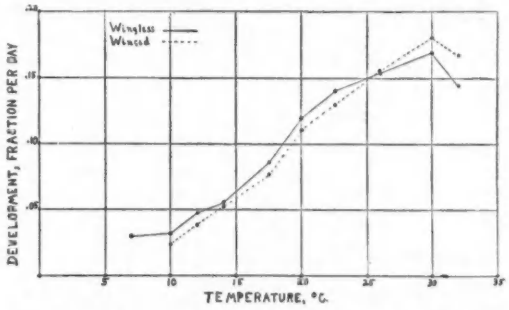


Fig. 2. Constant temperature and development, laboratory results.

In other experiments a few incomplete figures were secured. At 14° C., 5 wingless aphids produced 17 young in 2 days, early in adult life; at 10° C., 4 young wingless adults produced 11 young in 3 days; these records show the same trend as those above.

At 5° C., 10 vigorous wingless adults produced 2 young, and 35 nymphs cast 4 molts, in 2 days; at 4° C. the same aphids cast no molts and produced 1 young in 2 days; no sign of development was seen in 2 days at 3°. In view of the difficulty of rearing at 7° C., it seems doubtful that complete development could take place at 4° and 5°.

At 30° depressing effects of high temperature are seen; at 32° there is considerable decrease in life length, total young and reproductive rate, and some in developmental rate, which becomes variable. Adults maturing are smaller than at lower temperatures; 7 typical ones averaged 1.31 mm. in length, .53 mm. in greatest width. Two nymphs were reared at 33° C. Nymphs failed to mature at 34 to 35° C., though some lived 7 days. At 34 to 35° C., adults produced a number of young the first day in the cabinet, and a few afterwards; at 37° and 38°, they produced a few young the first day, none afterward; at 40°, none at all. It has been noted several times that adults moved from moderate temperatures to 32° to 35° C. reproduce rapidly the first

16 to 24 hours and only slowly afterwards; this is similar to effects found by Cook (1927) in cutworms.

One experiment in alternating temperatures, 22° and 12°, was carried out; periods of 8 and 16 hours each were used, so arranged that an equal time was spent at each temperature for the period. Wingless young developed in 9 to 11 days, 14 averaging 10.1 days; 5 wingless adults averaged 2.48 young per day for 9 days. It will be seen that these rates are higher than would have been expected from the average, 17°, but not much higher than would be expected from a combination of two equal periods at 12° and 22°.

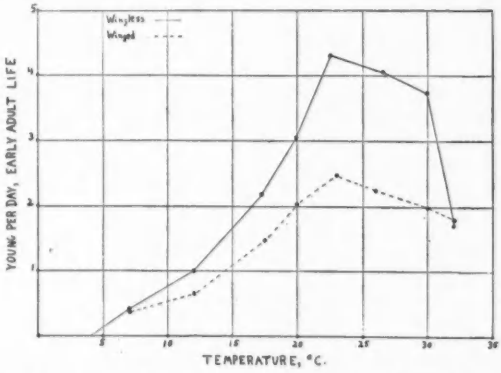


Fig. 3. Constant temperature and reproduction, laboratory results.

Figures 2 and 3 express graphically data on development, and on reproduction early in adult life, at constant temperatures. It is seen that development follows a fairly straight line within the range of moderate temperatures; but reproduction rate follows a somewhat curved line, the highest point being at 22-23° C. The high reproduction rate at this temperature has been observed in two sets of experiments. Results suggest that the winged form is adapted to slightly higher temperatures than the wingless. A majority of the nymphs died at 7° and 32°; those maturing may have been selected groups, and results at these extremes may not be as reliable as at the other temperatures in plotting the temperature-development curve.

Length of adult life and reproduction period did not vary significantly with the parents used through the medium temperature zone; except that with wingless adults it averaged lower with the exceptionally rapid reproduction at 22° to 23° C. This latter fact has been observed in two experiments. At 30° life-length was significantly decreased; at higher temperatures it was much shortened. Below 17° C. adult life was somewhat lengthened. Adding time of nymphal development and adult life as recorded, it will be seen that total life is from 3 to 6 weeks at moderate temperatures, and may approach or exceed 2 months in cooler seasons.

Total number of young per adult is greatest at 20° to 27°, and is reduced at higher and lower temperatures. At higher temperatures life is shortened and reproductive rate reduced. At lower temperatures the reproductive period is lengthened, but not in proportion to reduction of reproduction rate; hence total number of young must be smaller. The out-door rearing also shows this; in April, May and October wingless parents averaged 27.8 days reproduction and 27 total young; while from June 1 to September 15 averages were 24.1 days and 60.3 young, respectively.

Rate of population increase depends mainly on rate of development, and on reproduction rate early in life. Both are high between 20° and 30° C.; reproduction is most rapid at 22° to 23°, development at

TABLE V.

ASSOCIATION OF TEMPERATURE AND APPEARANCE OF WINGED FORMS OUTDOORS.

Period	Mean Temperature, °F.	APHIDS BORN IN PERIOD, OF WINGLESS PARENTS	
		No. Reared	% Winged
1926.			
August 1 to 31	70.5	125	4.0
September 1 to 23	61.0	145	29.0
September 24 to October 31	48.5	21	0.0
1927.			
April 1 to May 24	51.0	30	0.0
May 25 to June 19	59.0	55	63.6
June 20 to July 15	72.0	34	14.7

30°. Increase is hence very rapid from 22° to 30° C., or roughly 70° to 85° F. At varying out-door temperatures the range will probably be a few degrees lower. Acceleration with alternating temperatures should allow rapid increase at an average of a little below 70° F.; and at varying temperatures averaging above 80°, maxima are likely to be injurious on hotter days. Results showing the depression of reproduction in the south in summer have already been cited. Population increase will be taken up more fully later.

EFFECTS ON PROPORTIONS OF BIOLOGICAL FORMS.

Ewing (1926, citing earlier work), Ackerman (1926), and the writer (Wadley 1923), all using *Rhopalosiphum prunifoliæ* Fitch, have noted effects of constant temperatures on percentage of winged aphids. All found that unusually few winged forms appeared at 65° F., and unusually many at about 60° F., as compared with other temperatures. In the writer's work (1923), a constant temperature of 60° could not be conveniently attained; hence a slightly variable temperature averaging 62° F. was used.

In the outdoor insectary, winged forms of *Toxoptera graminum* appeared in considerable numbers, in spite of good nutrition, in spring and fall. The length of day differed in the two periods; and aphids reared in the greenhouse in higher temperatures, but the same day-length, in May and June, were not affected; hence it seems unlikely that length of day was the decisive factor. From results on other species of aphids, it seems that temperature variations might account for the increase of winged aphids.

It has not been possible to carry on a comprehensive investigation of influence of temperature on percentage winged. Some work has been done in bringing half-grown nymphs destined to be wingless, into various temperatures from 10° to 26° C., allowing them to mature and

TABLE VI.

TEMPERATURE AND PROPORTION WINGED IN LABORATORY.

TEMPERATURE, °C.	SECOND GENERATION		THIRD GENERATION		FOURTH GENERATION	
	Wingless	Winged	Wingless	Winged	Wingless	Winged
12	14	0	...	...	...	...
14½	42	0	...	...	...	...
17	41	0	20	1	...	...
22	21	0	...	...	...	...
27	7	0	24	0	...	...
32	10	0	...	...	...	...
Alternate—7 and 22	23	0	26	1	...	...
Alternate—12 and 22	21	10	32	5	18	8

produce young, and rearing the young. All series were similar; very few winged forms developed. As it was seen that temperature influence did not appear strongly in the first generation, some were reared from birth under controlled temperatures; some of their progeny were then reared for a generation or more, using wingless parents. The results are given in Table VI.

The alternating temperature experiments were at the higher temperature 14 to 15 hours per day.

The temperature alternating between 12° and 22° shows a definite tendency to produce winged forms, and this accords with insectary results. Other temperatures have not shown such a tendency.

Temperature has some influence on the appearance of sexual forms, though shortened days seem to be the principal factor. High temperatures seem to prevent their development. They have appeared under moderate to cool temperatures, with shortened days; both in the outdoor insectary in summer, with days artificially shortened (Table XI), and in the greenhouse in fall and winter with natural short days (Table X). They have not appeared, except a few males, in the greenhouse

in summer, with artificially shortened days and higher temperatures (Table XI). They have not appeared with longer hours of light and cool conditions, either in the insectary (April and May) or in the temperature laboratory (Table VI). The highest temperature in which they have been produced averaged a little over 70° F. with minima occasionally below 60° F. With temperatures averaging 73° to 76° F., and minima usually above 65°, no oviparous females and only a few males have been reared. This was checked by parallel rearing in warm and cool greenhouses, averaging 76° and 66° F. in the fall of 1927. In the former, no sexual forms were reared among 109 aphids; in the latter, 20 out of 86 were sexual forms after the first two generations. When Toxoptera was moved from the cool to the warm greenhouse, no more sexes were reared after one generation. It appears that their development is retarded or prevented by cold as with other forms, since they failed to develop outdoors in the fall and developed in the greenhouse, just as did the parthenogenetic forms; Table III shows a few cases indicating retardation.

Effects of Extreme Cold.

Some knowledge of the power of Toxoptera to endure cold has been gained from observations in the field, and from the literature. Viviparous forms seem to winter regularly in southern states, and less often as far north as Indiana. Where wintering occurs the temperature is high enough for slow development at times during the winter. Where 0° F. has been recorded, Toxoptera has survived only with protection, in the writer's observations. It seems likely that temperatures among plants on the ground are often not quite as low as recorded atmospheric minima.

In the insectary in November 1926, an adult and 7 nymphs died after 12 days continuously below 42° F., with a minimum of 8° F.; one remaining nymph survived 6 days longer, dying when —1° F. was reached. In November 1927, only one adult was carried into the winter; it died after 11 days below 42° with a minimum of 10° F. The pot-cages used gave practically no protection against cold. In an outdoor cage, considerably sheltered by snow and nearby buildings, the lowest winter temperature reached was 9° F. and the temperatures were usually between 20 and 30° F. Even here all of a colony of several hundred Toxoptera died before January, and colonies placed in the cage later in the winter died within a month. Similar results were obtained in an unheated greenhouse of about the same temperature range. Aphids were observed to withstand exposure to 8° or 10° F., but seemed unable to endure prolonged cold.

Observations under controlled conditions were carried out in the temperature laboratory. Preliminary experiments showed that all stages and forms were somewhat similar in resistance to cold; but that wingless parthenogenetic females were slightly hardier than large nymphs and winged females. Small nymphs were more variable than other stages. Only a few sexual forms were available; a male and 2

females proved unable to survive —11° C. for 3 hours, though some viviparous forms survived this. Of aphids hardened at 0° to 4° C. for 36 hours, then exposed to —12° C. for 2 hours, 13 out of 40 survived; of aphids fresh from the warm greenhouse, only 6 out of 80 survived. Aphids fed on plants hardened to cold but not themselves hardened, were as tender as those fed on non-hardened plants.

In later experiments aphids were hardened over night at 0° to 4° C. They were placed in vials (pre-cooled for the shorter periods) with bits of leaf, and put in a cabinet at the desired temperature. Vials were withdrawn at the end of various time intervals. For the sake of brevity, only critical points found are stated. Where the data do not yield the exact point, a range of time is given instead of an interpolated time. Table VII shows relations of time and fatal cold.

TABLE VII.

TIME AND FATAL COLD.

Temperature, °C.	Temperature, °F.	Total No. Aphids Used	Maximum Time all Alive, Hours	Time About Half Killed, Hours	Minimum Time all Dead or Paralyzed, Hours	Minimum Time all Brown on Thawing, Hours
—23.3	—10	50	....	0.02 to 0.03	0.08 to 0.17	0.33
—20.6	— 5	90	....	0.05	0.25	0.75
—17.8	0	54	....	.....	0.50	1.00
—16.1	+ 3	90	....	0.25	0.75	....
—15.0	+ 5	95	....	0.50	1.00	....
—12.2	+10	90	....	2.00	3.00	....
— 9.4	+15	50	2	5 to 10	15 to over 20	....
— 6.7	+20	146	21	72 to 96	120*	....
— 3.9	+25	50	96	96 to 120	168	....
— 1.1	+30	77	144 (6 days)	240 (10 days)	264 (11 days)	....
+ 1 to +3	+33.8 to +37.4	21	264 (11 days)	408 (17 days)	672 (28 days)	....

*Chimney cages instead of vials used for the longer periods.

It was found that when only part of a group of aphids was killed by cold, some of the survivors appeared normal but moved only feebly. They lacked coordination, and several trials showed that they always died in a day or two. These were counted as killed, in tabulating results.

The freezing point was taken with a thermocouple, by the rebound method, which is based on Bachmet jew's work (1901). A piece of glass tubing was sealed at one end, and filled with live aphids. The thermocouple was introduced, macerating the aphids more or less, and the mouth of the tube wadded with cotton. Several trials gave freezing points from —1.5 to —2.5° C. (29.7 to 27.5° F.). A second

but much less definite rebound, often represented only by a slowing up of temperature decline, occurred at about —14° C. When exposed to a temperature well below this point, all aphids turned brown on thawing, uniformly through the body. This indicates disruption of tissue or cells, perhaps associated with the lower rebound. At —12° to —16° C., some turned brown and some remained green, though dead or paralyzed; this may indicate individual variation. Above these temperatures they did not turn brown unless dead for some time. This lower rebound has a definite relation to time to kill at different temperatures; the higher, more definite freezing point has not (Fig. 4).

Webster and Phillips (1912) tell of eggs wintering successfully in Indiana; Washburn (1908-B) records finding some in Minnesota in the spring, most of which were dead, but a few of which hatched.

TABLE VIII.

TIME AND FATAL HEAT.

Temperature, °C.	Temperature, °F.	Maximum Time all Survived, Hours	Time Fatal to About Half, Hours	Minimum Time all Killed, Hours
41	105.8	.25	.33	.67
40	104.0	.50	.50 to 1.00	2.00
38	100.4	1.00	3.00	5.50
35	95.0	16.00	.....	.....

The writer secured 60 eggs of normal appearance in the greenhouse in November, 1926, on plants and on the chimneys used for cages. Some were kept in the insectary, exposed to temperatures reaching —20° F.; others were kept in an unheated greenhouse, the minimum being 0° F., and temperatures below 10° occurring only once. All failed to hatch in the spring. Dead embryos were found in some on dissection. Results were similar in 1927. Temperatures under six inches or more of snow were not below 12° F., seldom below 20°, and it would seem that some might survive with such protection. Eggs seem not to be fully hardy in Minnesota, though there is a possibility of some surviving.

EFFECTS OF EXTREME HEAT.

Experiments and records in literature showing depression of development and difficulty of rearing at high temperatures have been noted. Lefroy (1908) and Moore (1914) note difficulties in passing the summer in India and South Africa; they note a root-feeding habit in hot weather.

In one case a greenhouse compartment was accidentally heated to over 100° F.; some Toxoptera on oats growing in a flower pot standing on soil, left the plants and clustered on the soil under the pot. In another case, in a cage kept at 40° C., aphids left the plants for the soil; later, when the soil became dry, they returned to the plants.

Heat avoidance is evidently a well-marked feature of their behavior, and may be related to the root-inhabiting noted in hot climates.

In testing for a quickly fatal temperature a vial containing a thermometer and aphids on a green leaf, was placed inside a larger vial in a beaker of water gently heated. Above 30° C. the aphids were restless, and above 35° they often left the leaf, moving almost frantically as the temperatures rose farther. Their movements became aimless at 41° and ceased at 42°. Nearly all were revived successfully after one minute at 42°, but none survived 30 seconds exposure to 43° C. (109.4° F.).

All stages seemed to endure heat about equally except small nymphs. In one case at 35°, 8 adults and large nymphs all survived 16 hours while all small nymphs died. In tests, adults and large nymphs on pieces of leaf were put in vials which were placed in a Carrier cabinet. Table VIII shows relations of time and fatal heat.

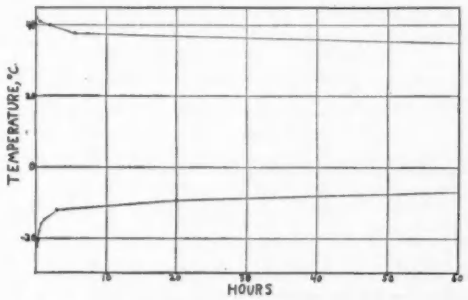


Fig. 4. Time and fatal temperature, laboratory results.

There is not a large class of apparently paralyzed aphids intermediate between those killed outright and survivors, with heat, as there is with cold. Some such have been seen, however. When paralyzed by heat, part may recover; of 24 placed on plants, 11 recovered.

Some trials were also made in putting pot-cages with Toxoptera on growing plants, in the cabinets; they did not die as quickly as in vials. All were killed in 14 hours at 40° C. At 34° to 38° adults lived one to several days and some reproduction occurred, as already noted. Colonies would quickly die out at such temperatures, as adults are short-lived and nymphs fail to mature. Thermometers were used within these cages. The cause of longer survival on growing plants is not known; it may be food or moisture supply, or lower temperatures on the leaf.

Fatal temperature and time are graphically shown in Fig. 4.

EFFECTS OF HUMIDITY.

Sap-feeding insects are evidently not likely to be directly affected by humidity; indirect influences result from the connection with precipitation and food supply. Adverse summer conditions are associated with low relative humidity. Headlee (1914) found *Toxoptera graminum* Rond. little affected by relative humidity ranging from 37 to 100 per cent.

No influence of humidity can be traced from greenhouse rearing and hygrographic records. In late spring and summer, day-length and temperature were favorable for reproduction; but humidity was lower in late spring owing to use of artificial heat. Reproduction and development were very similar in the two periods. In April and June, 1927, humidity averaged 48 per cent and 67 per cent, respectively, and little difference was observed. Greenhouse humidity averaged only about 30 per cent for over a month in the fall of 1927. The food

TABLE IX.

HUMIDITY AND ADULT ACTIVITY.

	IN MOIST CHAMBER—100%			OUTSIDE, COMPARABLE—50%±		
	No.Cases	Average	Range	No.Cases	Average	Range
Adult life.....	3	14.3 days	13 to 18	4	15.0 days	6 to 22
Total young...	3	22.7	12 to 36	4	29.2	18 to 37
*Reproduction rate per day..	4	1.8	.....	4	2.5	.....

*Based on reproductive period, not on total adult life.

plants did not thrive well, and were renewed often. *Toxoptera graminum* developed normally, except for the production of more winged forms than usual, which would be expected from the condition of the plants. A wet bulb thermometer reading, taken with great care in the type of latern globe cage most used, showed a relative humidity of 45 per cent as compared to 39 per cent outside, and indicated that cage conditions were much like those outside.

Table IX gives a summary of rearing results, in a moist chamber with saturated air, in the greenhouse in the late winter of 1927; compared with rearing just outside in a humidity of about 50 per cent. The parents used in the moist chamber were sisters of those used outside in a regular generation series.

The reproduction rate in the extreme humidity was somewhat depressed; the exact time required for development was not secured, but it did not differ greatly from the check.

The species seems practically unaffected by moderate variations in relative humidity and but slightly affected by extreme variations.

EFFECTS OF LIGHT.

Toxoptera graminum has been reared with ease in natural light coming through wire screen, cloth, mica, and common glass. In the temperature laboratory, large numbers and consecutive generations have been reared without much difficulty by both ordinary tungsten lights and nitrogen-filled "daylight" bulbs, although food-plants did not thrive very long. The species has done well in every light tried which was favorable to its food plants. No experiments on quality of light have been carried on. More than 50 generations of Toxoptera have been reared under glass, and oats have yielded viable seed in

TABLE X.

REPRODUCTION AND DAY LENGTH.

Month	No. Reared During Month	Percent Sexes Among those Maturing	Percent Winged	Reproduction Rate Per Day, Average	Average Temperature, °F.	Averave Day-length, Hour
January	125	23.2	8.8	1.9	68.5	9.3
February	152	13.2	16.4	2.3	72.5	11.3
March	75	6.7	32.0	1.7	71.0	11.7
April	104	0.0	1.0	3.1	72.0	13.6
May	187	0.0	1.6	3.5	74.5	14.3
June	184	0.0	5.4	3.7	76.0	15.5
July	224	0.0	2.7	3.6	75.0	15.2
August	144	0.0	0.0	2.9	73.5	14.0
September	140	0.0	22.9	2.6	73.0	12.8
October	184	6.0	13.6	1.7	70.0	10.9
November	180	30.0	12.2	1.8	71.5	10.0
December	43	34.9	2.3	1.7	69.0	8.7
April to August, inclusive	.....	.....	.....	3.4±0.084	74.2	.....
October to March, inclusive	.....	.....	.....	1.8±0.055	70.4	.....

quantities; hence it may be said that daylight coming through window glass is sufficient for the needs of this aphid and its food plants.

The quantity of light per day is important. Garner and Allard (1922) did pioneer work on connection of day length and reproduction in plants. Marcovitch (1924) and Shull (1926, 1927) show that sexual forms appear in several aphid species in response to shorter light periods; also that winged forms are more numerous with less light. Davidson (1924), using *Aphis rumicis*, reared sexes in the greenhouse in winter; they failed to appear when the day was lengthened by artificial light. Washburn (1908-B) noted smaller families of *Toxoptera graminum* Rond. in winter, in greenhouse rearing; Hunter (1909) found reproduction reduced when the sexes were developing.

In the present work, sexes did not appear in outdoor rearing, development apparently being checked too soon by cold, but did develop in the greenhouse all through the winter.

In Table X are given rearing records, in the greenhouse from September 22, 1926 to September 12, 1927. The daily reproduction rate of all wingless females is included. Winged females did not produce sexual progeny in the present work. The rate all through adult life is used, as it seems as comparable for this purpose as that early in life and gives more records. A few females caged on wheat during the winter are included. They differed little from those on oats in the matters considered, though shorter lived. Temperature records were taken with a hygrothermograph most of the time; bi-daily thermometer readings and a recording thermometer were used for short periods in the fall. Day lengths are calculated from data for St. Paul in U. S. Weather Bureau Bulletin Q.

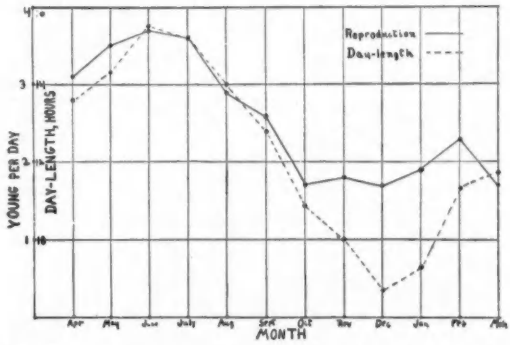


Fig. 5. Average reproduction in greenhouse, and day-length, by months. (Temperature varied but little.)

The association of day length with reproductive rate through the year is graphically shown in Figure 5; with percentage of sexes in Figure 6. It has been found that sexes do not appear until a few weeks after conditions become favorable, and continue to appear for a short time after the favorable conditions are removed.

Sexual forms also appeared in greenhouse rearing in fall and early winter, 1927. Winged females produced no sexual progeny; three in spring and summer averaged 2.5 young per day and a total of 37; four in winter averaged 1.6 per day and a total of 29.

It will be noted that the reproduction rate from October to March is lower than that from April to August, and that the difference is very significant and too large to be explained by the small difference in temperature. The differences between months within each period are usually not significant. September seems definitely transitional as to reproductive rate, especially in the latter part, and is omitted from the comparison. Thirteen females in the greenhouse in fall and winter show almost exactly the same length of life and reproductive period as 19 in spring and summer. The total number of young is much smaller in the former period, being proportional to the reproduction rate. The time required for development was longer in the winter period

(10.0 days ± .363 as compared to 7.4 ± 0.153), but the difference may not be significant when allowance is made for the difference in temperature.

Experiments in day-shortening, darkening pot-cage colonies of Toxoptera part of the day by inverting large flower pots over them, were conducted in the summer of 1927. For two months a maximum and minimum thermometer was kept under the cover; this was discontinued when it was found that the temperature differed very little from that just outside. Experiments showed that feeding and reproduction took place in the dark. For days of 8, 9, and, in a few cases, of 10 hours, covers were put on in the afternoon and removed in the morning; in other experiments they were put on in the afternoon and

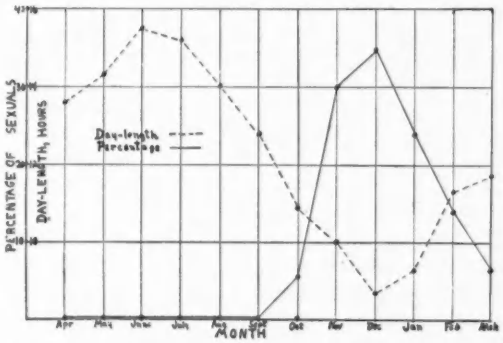


Fig. 6. Day-length and percentage of sexual forms among those reared in greenhouse, by months.

removed after dark the same evening, so that the cages were covered only a few hours and were exposed to normal dawn. Consecutive generations were reared in each day-length, so that the line was kept under the given conditions; wingless parents were used. The 9-hour cage was run in the insectary, with temperatures averaging a little above 70° F., and minima often below 60° F. The others were run in the greenhouse, with temperatures averaging about 75° and minima seldom below 65°. These higher temperatures appeared to prevent production of sexes, as already stated. In the insectary with a 9-hour day, both sexes were reared in July and August. Data from these experiments are shown in Table XI. Data on proportion of forms includes in some cases one generation after treatment ceased, as it was found that its effects persisted in one generation.

It is concluded that days shortened beyond a certain point produce a definite drop in reproduction rate, and associated with this at suitable temperatures is production of sexual forms. This point appears to be between 11 and 12 hours, and notes indicate that with natural day-length it is near 12. The drop in reproduction begins at once after the days are shortened; sexes do not appear until two generations later. Tables X and XI and Figure 5, suggest that the reproduction rate

does not vary much from 8 to 11 or 12 hours, or from 14 to 16 hours, but that there may be some gradient in rate from 11 or 12 to 14 hours. Data are not yet sufficient to determine whether percentage of sexes varies with day-length, below 12 hours.

Winged forms show an increase with 8- and 9-hour days; these results are similar to Shull's (1927); they also showed a marked increase at 12½ hours. The latter tendency is reflected in greenhouse results in March and September; but in September the winged forms were largely among some brought in from outside at the start, hence were influenced by temperature also.

The effects of day-length on development of the sexes is important in studying the economic status of the species, and its effects on develop-

TABLE XI.

REPRODUCTION WITH ARTIFICIALLY SHORTENED DAY.

Day-length, Hour	Period	Place	Reproduction Rate Per Day	Total Number Reared	Males, Percent	Oviparous Females, Percent	Winged Females, Percent
8	April 25–Aug. 2	Greenhouse	2.3	129	2.3	0.0	35.6
9	June 25–Sept. 12	Insectary	2.2	350	2.6	6.3	39.4
10	Aug. 1–Oct. 31	Greenhouse	2.3	286	0.3	0.0	13.3
11	Aug. 1–Oct. 20	Greenhouse	2.9	157	3.2	0.0	20.4
12	Aug. 1–Sept. 30	Greenhouse	3.3	107	0.0	0.0	0.9
12½	Aug. 1–Sept. 12	Greenhouse	3.0	206	0.0	0.0	56.8

ment of winged forms may also be of some importance. The drop in reproduction with short days does not appear to be of importance in the field, as short days occur only when cold slows up or prevents reproduction. It is important, however, in interpreting results of greenhouse rearing in winter, with natural light. It may well be asked if cloudiness alters the day-length effective in producing sexes; fragmentary data indicate that such may be the case. Kelly (1917) found no sexual forms in the field in northeast Kansas in 1907, but found some in 1908; Hunter (1909) reared them late in October, 1907, and early in October, 1908, in the same region. They were more abundant in the field in Indiana in 1908 than in 1907 (Webster and Phillips, 1912). The fall months, especially September, were cloudier in 1908 than in 1907 in both areas (Monthly Weather Review). Sexes appeared over considerable periods of both decreasing and increasing day-length, indicating that the length and not the change of length is the important factor. It is obviously not entirely dark at night in the greenhouse; the effective shortening of the day must be due not to long night periods of absolute lack of light, but to periods of light below a certain critical intensity. Cloudy conditions may increase the length of that period of the day below this intensity, thus lengthening the effective night.

EFFECTS OF VARIOUS WEATHER PHENOMENA.

Rain.

An apparent association of outbreaks of *Toxoptera graminum* with dry weather, and apparent diminution in numbers during rainy spells, suggested investigations as to the cause. High humidity proved not to be very detrimental; several authors cited have mentioned decrease due to rain. Of two areas, one sprinkled three times a week and one not sprinkled, in a bed of oats in the greenhouse, Toxoptera graminum increased in the unsprinkled area and barely persisted in that sprinkled.

TABLE XII.

Effect of Sprinkling on Numbers.

Numbers	Small Nymphs (1st and 2nd instars)	Large Nymphs	Adults
Before sprinkling	127	92	50
After sprinkling	84	53	29
Succumbed	43	39	21

The sprinklings were faster than natural rainfall, ¼ inch of water being given in less than a minute. In 3 cases colonies in pot-cages were sprinkled and counts made.

TABLE XIII.

Effect of Rains on Numbers.

Experiment	Date	Kind of Rain	No. of Toxoptera		No. on Checks
			Before	After Rain	
First	May 12	Moderate shower	39	17	43
"	" 12	Hard rain, hail	17	None seen	43
"	" 19	Fine misty rain	15	11	162
"	" 27	Moderate shower	73	45	Plants dead
Second	July 3	Hard shower	166	106	54
"	" 13	Hard shower	.....	338	347
"	" 16	Hard shower	.....	243	419
"	" 23	Several light showers	.....	125	609
"	" 28	Several light showers	.....	8 (heading)	126 (injured)

The action of sprinkling water being established, tests were made by exposing large pots of infested oats to actual rains. Two experiments were made, in May and July. Checks not exposed to rain were run.

In the first test small oats were used; in the second, larger plants, of 3 leaves, growing vigorously. The plants exposed to rain in the second test headed normally, aphids leaving at about heading time,

while the check plants were killed by Toxoptera after becoming 8 to 10 inches high.

In small oats, Toxoptera may be almost entirely controlled by rain; but in 2 weeks with little rain, as from May 12 to 27, considerable injury may develop. In larger and denser growth complete control will not occur, but rain may hold back infestation. Rains 2 or 3 times a week probably hold *Toxoptera graminum* well in check. Aphids washed off are often found partly buried in the mud; others are able to regain a footing, and still others are doubtless completely buried. Equal rains probably have a stronger controlling action in cool than in warm weather, because losses are replaced by reproduction more slowly. Glenn (1909) mentions winter rain as especially detrimental.

Snow.

Webster and Phillips (1912) record successful survival of cold spells by *Toxoptera graminum* with snow protection. In several cases a lantern-globe pot-cage with oats infested with Toxoptera was filled with snow sifted gently in, and set in an unheated greenhouse with the temperature near freezing. On thawing, survival was observed (Table XIV).

TABLE XIV.

Time Under Snow	Survived
1 day	Part
2 days	Part
16 hours	12 out of 20
10 days	1 out of 18
18 days	0 out of 20

Covering with snow is not of itself fatal to all the aphids, though some stick in the mud on thawing. It may enable the species to pass short periods of severe cold. Temperatures under snow are surprisingly mild; a recording thermometer showed that in 1926-27, under 6 inches or more of snow, the temperature was usually between 20° and 30° F., with a minimum of 12° F., at St. Paul. However, in Minnesota the cold is too prolonged for survival under snow, as *Toxoptera graminum* dies in a few weeks even at the freezing point.

Wind.

Field observations, and a few greenhouse experiments with an electric fan, indicate that Toxoptera thrives in windy localities as well as sheltered ones; except that cold weather can be withstood better with shelter. The most important effect of the wind is as a stimulus and an aid to migration. Some observations were made by the writer and others in Minnesota in 1926.

Toxoptera graminum was seen flying north, southeast, and west, in every case with the wind. F. C. Hottes and T. S. Aamodt, graduate

students, saw swarms of the aphids rise from infested grain as a breeze sprang up, settle as the breeze died down, and rise as it blew once more. Webster and Phillips (1912) and other workers have observed association of flight with wind; Kelly (1917) notes that they change direction when the wind shifts. Toxoptera seems a weak flier in still air, but appears to fly with little effort in a moderate wind. The Chitrovo soaring coefficient (Collins 1915) is about 135 for the winged form; this compares with about 500 for young gipsy moth larvæ, which are easily transported by wind, and the surface of winged aphids seems well arranged for buoyancy in an air current. These observations indicate that the species is largely dependent on the wind as to direction and distance of flight.

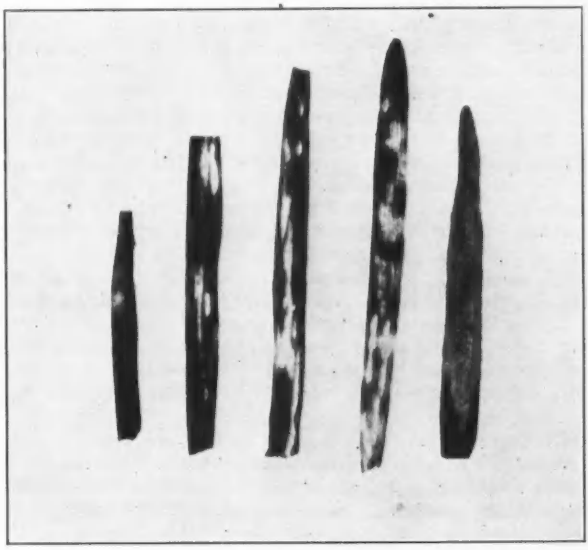


Fig. 7. Oat leaves in varying stages of injury from feeding of Toxoptera.

FOOD RELATIONS.

Under this heading may be considered injury caused by feeding, plant species furnishing food, reaction to food plants, and other nutritional factors.

Injury.

This species is much more injurious in proportion to its numbers than other grain aphids observed. Its feeding causes a peculiar and characteristic injury to its food-plants, (Fig. 7), which has been studied

by the writer (Wadley, 1929). Pale spots with red centers developed around feeding punctures. Injury invariably followed prolonged feeding and was roughly proportional to amount of feeding. Neither recovery, nor spread for long after feeding ceased, was observed. Injury was similar on various food plants. Paleness was apparently due to destruction of chlorophyll, while red spots were caused by reddening of the leaf-cell nuclei. A water extract of frozen Toxoptera slowly decolorized a solution of refined chlorophyll. After heating the extract lost this power. It seems likely that an enzyme produced by the aphid is the cause of the destruction of chlorophyll.

Food Plant Species.

Webster and Phillips (1912) list about 60 food plants; a few others are mentioned by Hunter (1909), Moore (1914), and Van der Goot (1915). All the food plants recorded are of the grass family, with rare exceptions. They include the common small grains, rice, corn, sorghum, millet and many annual and perennial grasses. Few direct statements are found in the literature as to the degree of infestation of different species. By far the majority of serious infestations recorded have been on oats and wheat. In some cases injury to barley and rye has been recorded. Young corn (Kelly, 1917) and sorghum (Hayes, 1922) have been temporarily infested by Toxoptera leaving dying oats or wheat nearby, but are usually not attacked. Bluegrass (*Poa pratensis*) has been injured in a few cases (Webster and Phillips, 1912; Garman, 1926) and seems to be a favorable host. Orchard grass (*Dactylis glomerata*) is mentioned by several workers, and Johnson grass (*Sorghum halapensis*) by Moore (1914), as favorable.

In the present work severe injury to oats and wheat has been seen; barley and rye have not been observed to be infested except when close to heavily infested wheat and oats. *Toxoptera graminum* has been found on wild oats (*Avena fatua*) in the field; small numbers have been found on bluegrass, corn, quack grass (*Agropyron repens*) and pigeon grass (*Setaria glauca*), when near infested grain. The species has been reared with some difficulty on Muhlenbergia sp. probably racemosa, which is probably a new food plant record. Many other grasses have been observed without finding Toxoptera.

The species can be accounted for throughout the year on the grass family; the sexes are produced readily on these plants, and no evidence has been found of other host plants alternating with grasses.

Reaction to Food-Plants.

The survey of the literature and the field observations noted would indicate that injury is greatest to oats and wheat, and that other plants are infested to a small degree. The insect has often been injurious from the Carolinas to Texas and Oklahoma, and sometimes in the regions to the north. The outbreak of 1926 extended to the Dakotas, Minnesota and Wisconsin. Injury in all these regions would imply that oats of most common cultivated types, both winter and spring varieties of *Avena sativa* and *A. sterilis* (Rustproof type); and

common wheat of hard winter, soft winter and hard spring types, have been injured; since all are widely raised in some parts of the region.

Minota, a white variety of oats, has been used in general rearing. In several hundred cases there has seldom been a failure to increase rapidly on it; a majority of nymphs born have matured and over 60 consecutive generations have been reared. Minturki, a hard winter variety of wheat, was also used for about 8 months with similar results. Reproduction was as rapid as on Minota oats, but adult life was shorter, families were smaller, and development appeared to be a little slower. The oats seemed to be somewhat better suited for the aphid than the wheat, though the difference was not great. Several other varieties of

TABLE XV.

Plant Species	Number Trials	Cases in Which				Duration of Colonies, Days
		First Generation		Second Generation		
		Was Born	Matured	Was Born	Matured	
Rye	8	4	1	1	1	1 to indefinite
Barley	7	3	1	1	1	2 to 29
Corn	1	0	0	0	0	2
Sorghum	1	1	0	0	0	3
Bluegrass	14	12	6	6	6	1 to indefinite
Orchard grass	4	4	2	2	1	2 to 56
Elymus canadensis	2	2	1	0	0	2 to 12
Bromus inermus	1	1	1	1	0	26
Muhlenbergia	6	5	3	2	2	1 to 42
Quack grass	6	1	0	0	0	2 to 11
Pigeon grass	2	1	1	1	0	5 to 34

oats, representing the Kherson, Rustproof, and Gray Winter types; and of common wheat, representing hard spring, soft red winter, and white types, were tested in a single set of experiments in pot-cage rearing. On all these, adults reproduced rapidly, half or more of the first generation nymphs matured, and a large and vigorous second generation killed the plants. On Little Club, a variety of the club type of wheat, often regarded as a subspecies, results were similar. On Mindum, a variety of the durum subspecies of wheat, and on common wild oats, rearing was somewhat difficult, less than half the nymphs maturing; but the second generation killed the plants. On Vernal, a variety of the emmer subspecies of wheat, the aphids refused to thrive; less than 10% matured, and no second generation developed.

Some other grains and grasses were tested. These included seedlings of corn, barley, rye, sorghum, *Bromus inermis*, and orchard grass; and transplanted bluegrass, quack grass, *Elymus canadensis*, pigeon grass, and Muhlenbergia. One to four adults were caged on the plants in each trial. On all these plants rearing was more difficult than on

oats and wheat; colonies often failed to become established or died out, total numbers reached were usually small, and plants were seldom killed by the aphids as with wheat or oats. Figure 8 shows graphically numerical increase in the most successful cases of rearing on bluegrass and Muhlenbergia as compared with an ordinary case on oats. Table XV outlines rearing results with these plants.

Barley and corn seedlings near heavily infested oats in greenhouse beds were attacked, but not colonized nor permanently injured. Barley seedlings among heavily infested oats in a tight cage were fed on till they wilted. Barley was peculiar in showing the typical Toxoptera injury but little; faint spots appeared, however, from prolonged feeding. Common six-row barley was used in most of the work, but in two trials a two-row variety was used; it did not differ much from the six-row. Bluegrass is a variable species (Piper 1924), and the variability seems to extend to suitability for Toxoptera. Several plants of ordinary appearance gave moderately good results in rearing, one not distinguishable from them gave more favorable results than the average, and on still another of similar appearance repeated trials ended in failure.

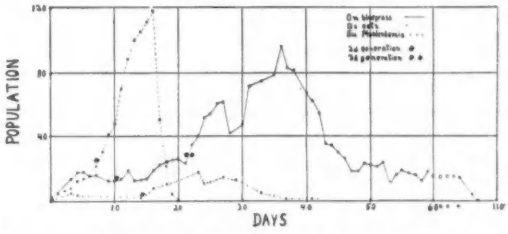


Fig. 8. Population increase on several food-plants.
(In greenhouse, temperature similar for all.)

A plant with finer blades than usual gave poor results while on a coarse-bladed one rearing was fairly successful. On timothy (*Phleum pratense*), red-top (*Agrotis alba*), crab grass (*Syntherisma*) and a barnyard grass not determined, feeding and reproduction were not observed in cages or near infested oats.

Plants studied may be tentatively divided into four classes. On preferred food-plants, rapid reproduction may continue indefinitely. Injury is obviously likely if multiplication is unchecked. Most types of wheat and oats studied will fall in this class, though some differences will be found among them. The next group may be termed second-choice food-plants; on them reproduction and growth are possible, but more or less restricted. Colonies are formed, but are often short-lived; on the other hand, individual plants sometimes live and remain infested a long time, because the aphids increase slowly. The chance of reaching injurious numbers is plainly not great. Orchard grass, Muhlenbergia, rye, the favorable types of bluegrass, and probably barley, emmer, Bromus and pigeon grass should be included from present data. The third class may be termed temporary food plants; feeding occurs, and there is a tendency to remain for a time, but repro-

duction is exceptional. From these experiments corn, sorghum, Elymus, quack grass, and some types of bluegrass should be included. Plants of this class may be injured when young if over-run by Toxoptera leaving nearby oats or wheat. On the fourth class Toxoptera has refused to remain long; timothy, red-top and other species should be included. Field observations and literary records agree in a general way with conclusions.

The only factors known to explain scarcity or abundance on different host species are increased restlessness and decreased growth and reproduction on the less suitable plants. The writer has not been able to detect sensory discrimination. Winged and wingless adults did not distinguish between barley and oats at first contact. White clover was fed on at first, though the aphids left in an hour or two. Hunter

TABLE XVI.

FACTORS IN SLOWER INCREASE ON DISTASTEFUL FOOD PLANTS.

Food-plant	Time Remained Adults from Oats, Days	ADULTS REARED ON PLANTS				
		Nymphal Period, Days	Average Size, mm.*	Reprod. Rate per Day	Reprod. Period, Days	Percentage Winged
Rye	1 to 5	11 to 14	1.33 x .60	0.9	4 to 10	.....
Bluegrass	1 to 9	10 to 11	1.23 x .51	1.4	3 to 10	39.7 (of 68)
Elymus	1 to 10	about 11	.....	.....	.....	.....
Orchard grass	1 to 5	9 to 10	1.22 x .50	.....	3 to 10	65.9 (of 44)
Muhlenbergia	1 to 9	11	.....	1.6	1 to 9	80.0 (of 5)
Pigeon grass	5 to 7	about 15	very small	0.7	3	.....
Bromus	1 to 5	8 to 9	1.35 x .42	1.3	2 to 4	.....
Oats, Comparable Cases	12 to 42	8 to 9	1.80 x .80	2.5	12 days or more	23.1 (of 117)

*Length and greatest width of live aphids.

(1909) records Toxoptera piercing toadstools; in this work one was seen attempting to feed on a pencil. The aphid feeds when it settles on a new plant, and leaves if the nutrition proves unsatisfactory.

The tendency to leave unsuitable food-plants, or to fail to thrive on them, is shown by Table XV. Large nymphs and young adults have been found dead on barley, rye, emmer, durum, wild oats and orchard grass. Decreased reproduction was partly caused by shortened reproductive period of the parents; these often reproduced at a normal rate for 1 to 3 days when put on unsuitable plant species, then nearly ceased reproduction, and left or died after a few days. It was also caused by the difficulty the new nymphs encounter in living on the plants, expressed in decreased percentage maturing, slower development, smaller size and lower rate of reproduction when mature. As the colonies became older winged adults, restless and not very prolific, became numerous. Data concerning these factors is brought together in Table XVI.

Many food plant records in the literature were probably made at times of great abundance and migration, when many species of plants were more or less briefly infested. A number of those should probably be classed as second-choice or temporary plants.

Other Factors.

Limited nutrition usually results in an increased percentage of winged aphids (Gregory, 1917; Wadley, 1923; Ackerman, 1926; Reinhard, 1927). With *Toxoptera graminum*, young nymphs born of wingless parents were confined in vials without food for given periods during development. They were carefully restored to the plants after starvation. This lowered the amount of nutrition (as they feed almost constantly when on the plant) without changing its quality. Several 8- and 16-hour starvation periods early in life did not increase the percentage of winged forms; even 24-hour periods were ineffective,

TABLE XVII.

Limited Nutrition and Proportion Winged.

	Total Number	Percent Winged
Nymphs, nutrition limited early in life	89	21.5
Checks	138	27.5
Unstarved progeny, of wingless adults starved early in life	35	82.9
Unstarved progeny, of wingless parents starved just before birth of offspring	73	69.9
Checks	77	15.6
Unstarved progeny of winged parents starved as above.	21	4.8
Checks	19	0.0

though they killed some nymphs. The progeny of wingless aphids starved when young, however, when reared with good nutrition, showed a high percentage winged. The effect of transferring to undesirable oat plants when quite young was next tried; also combinations of feeding on poor plants with starvation periods. These methods showed results similar to those of starvation alone.

Some aphids were starved by confinement in vials for 16 hours, shortly before progeny were born. Wingless nymphs about to mature, then wingless adults were tried. Their progeny reared on favorable plants showed a marked increase in winged forms, even when parents were starved for only one period the day before their birth. Starvation of winged adults, however, gave negative results.

Confinement in vials stops reproduction at once, but it is resumed within a few hours after restoration to the plants.

Poor nutrition may result from the food-plant being in poor condition, approaching maturity, or being of an unsuitable species, as well

as from complete deprivation of food. Reproduction on unfavorable species has been discussed. It has often been noticed that many winged forms develop on overcrowded and failing plants, and that reproduction is checked and nymphs with wing-pads appear as oats and wheat are heading.

Wingless adults reared with ample nutrition but placed on the test plants just before maturity were allowed to produce young. The rate of reproduction, and number of winged among the progeny, were noted. Some wingless progeny were later placed on favorable plants and their progeny reared. Results appear in Table XVIII.

TABLE XVIII.

REPRODUCTION AND PROPORTION WINGED ON UNFAVORABLE PLANTS.

Plants	Reproduction per Day, Parents	First Generation of Progeny		Second Generation (Favorable Nutrition)	
		Total Number Reared	Percentage Winged	Total Number Reared	Percentage Winged
Healthy oat seedlings	3.1	69	10.1	*	*
Same, but with dry soil	3.3	53	15.1	18	66.7
Seedlings, injured by previous Toxoptera feeding	2.9	33	24.2	50	86.0
Oat seedlings, unthrifty	3.1	34	20.6	28	42.8
Large plants, in joint, 4 leaves	3.3	70	21.4	28	21.4
Large plants, heading	3.2	13	15.4	21	28.6
Large plants, heading, later trial	.....	.....	.....	52	75.0
Young plants, check later trial	.....	.....	.....	52	25.0

*The first generation on healthy plants served as a check, as the aphids had been reared on such plants for several previous generations.

Daily reproduction was not much affected by varied nutrition, but adults soon left the heading plants and those classed as unthrifty. On these and on injured plants fewer nymphs matured. On the heading plants, only 13 out of 32 matured in the first trial; development was slower and the new adults were smaller than on others, and behavior in general was similar to that on second choice food-plants. These plants alone survived the experiment in good condition. It is of interest to note that plants just heading are less suitable for the aphids than younger plants, as at the heading stage they appear green and tender. The large plants just jointing, on the other hand, were still suitable.

It is concluded that all forms of curtailed nutrition produce a high percentage of alates; that the effect is seen in the succeeding generation. Curtailed nutrition, if severe, may be effective in wing-production as late as a day before birth, but is not effective after birth. Poor nutrition

seems not to affect rate of reproduction of vigorous aphids much unless it is severe, when it tends strongly to stop reproduction altogether. With plants of suitable species and age, but unhealthy, many winged forms develop and migration occurs; it may be hastened by collapse of plants. Factors influencing numbers on unsuitable plant species have been discussed; they appear to be similar with suitable species becoming too mature.

APPEARANCE OF BIOLOGICAL FORMS.

Having considered relations to physical factors, including nutrition, it is desirable to consider several subjects having to do with survival and increase of the species. These factors are characteristic of the species itself, though they are modified by environment, and are discussed under environmental conditions; they fall under the heading defined by Chapman (1925) as biotic autecology. First to be considered is the appearance of biological forms. These different forms are fundamental to the ability of aphid species to migrate and withstand the seasons.

Some factors affecting their proportions have been treated. They will be briefly brought together. Relations of the sexual and parthenogenetic forms, and of winged and wingless parthenogenetic females, are characteristic of the family. These relations might be expected to be governed by the same general principles throughout, with minor specific differences.

Winged and Wingless Females.

Differences between winged and wingless females seem less deep-seated than those between parthenogenetic and sexual forms. Wingless females are more abundant under favorable conditions. It is possible to rear nearly 100 per cent wingless regularly. Ewing (1926) has reviewed most of the recent work on factors affecting proportion of winged and wingless aphids.

The effect of parentage is pronounced with *Toxoptera graminum* Rond., as with other species. In the first year's insectary and greenhouse rearing, 293 young were reared from 15 alate parents; all but one were wingless. At the same time, progeny was reared from 67 wingless parents; 36 had from a few to 75% winged among their progeny, 31 had none. Of the entire progeny of the 67, about 12 per cent were winged. Winged parents produced nearly all wingless progeny even when nutrition was limited.

It has been shown that limited or unfavorable nutrition when endured by wingless aphids greatly increased the proportion winged among their progeny. A variable temperature averaging about 60° F. was associated with an increase of winged forms both in insectary and laboratory, as was a day-length of about 12½ hours; these indications are less clear cut and rest on fewer data than the conclusions as to effect of nutrition, and more work on the subject is desirable.

Brittain (1921), and Reinhard (1927), emphasize overcrowding as a factor increasing the proportion of winged aphids, and publish evidence that it has an influence independent of that of nutrition. It is hard to separate these influences; with *Toxoptera graminum* it is practically impossible, as a plant or part of a plant crowded with Toxoptera would be dead in a few days.

It is clearly established that the winged form of Toxoptera has a strong tendency to produce wingless progeny, and is little influenced in this by environment. The wingless form may produce 100 per cent wingless or nearly 100 per cent winged, and the percentage may be modified by environmental conditions. Limited nutrition gives the most positive results in increasing the proportion of winged forms and may produce them at any time in the season. The temperature effect observed would tend to produce migrants in the field at somewhat definite times in spring and fall, while the day-length effect would tend to produce them in September. The winged females seem to be inherently migratory, and any factor producing them is a cause of migration.

As observed before, with Toxoptera wing-production factors are not effective after birth, but must be applied to the parents. This agrees with results on the pea aphid (Gregory, 1917), and the potato aphid (Shull, 1927). However, with the melon aphid (Reinhard, 1927), the apple-grain aphid (Wadley, 1923 and others) and several other species (Shinji, 1918) wing producing factors may be effective after birth. The young, at least of wingless parents, must all be potentially winged; and some internal conditions, influenced by external factors acting before a certain critical stage, must govern wing development. Ackerman (1926) has studied internal difference in nymphs of the apple-grain aphid. With wing development are associated several morphological and physiological differences.

Sexual Forms.

Work on the history of the germ-cells of various aphid species, some similar to Toxoptera, is summed up by Wilson (1925). It is found that males differ slightly from females in chromosome number, and that the difference comes about in maturation. The oviparous female does not differ from parthenogenetic females in chromosome number; her ovaries are different, and she must be determined early in development. Stevens (1905) found maturation stages in well-developed aphid embryos; in a young female not quite mature containing large embryos, maturation of individuals two generations ahead may be taking place. If *Toxoptera graminum* resembles the species she used, which seems probable, factors producing sexual forms must be at work about two generations before the forms appear.

No environmental factors other than day-length and temperature have been observed to influence the production of the sexes. They have appeared under natural days of less than 12 hours, and artificially shortened days of 11 hours or less. Both sexes have appeared when the temperature averaged 70° F. or less; above this, only a few males

developed. These forms appeared each time these conditions of temperature and light were fulfilled. Day-length seems the dominant factor; the rearing of a few males with short days and high temperatures show a tendency to produce sexuals, but with long days and favorable temperatures no such tendency appeared. No influence of food-plants was seen, except that the two sexes were about equal in number in the line on oats, and twice as many females as males occurred on wheat. All sexes reared were the progeny of wingless females; none were found among 138 aphids reared from winged parents, in the greenhouse from October to March. (Compare wingless parents, Table X).

A few further facts may be recorded concerning these forms. They were not produced before the second generation, born under favorable conditions, and have not matured earlier than about a month after the onset of these conditions. This conclusion is drawn from 5 sets of experiments. They continued to appear in one generation after favorable conditions had been removed, in 7 experiments; in the second generation after conditions changed none were reared in 3 trials. Males and oviparous females appeared at the same time in the greenhouse in two winters, and in the insectary in midsummer when the days were artificially shortened. Of 12 families having 5 or more sexual forms, 9 included both males and females. Males appeared under a wider range of conditions, however, and might conceivably be produced without oviparous females. The majority of aphids were parthenogenetic even when sexes were developing; in the winter of 1926-27 in the greenhouse, about 20 per cent were sexes. Of 15 families of 20 or more aphids in this period, only one had no sexes, and only one had a majority of them. The sexual forms were often, but not always, among the later-born members of a family.

No evidence of reduction of vigor by continuous parthenogenetic reproduction, as suggested by Luginbill and Beyer (1918) is seen after over 60 generations. Comparable generation rearing in two years was done in the insectary in August and in the greenhouse in October. August results on reproduction and development show slightly more vigor in 1926 than in 1927; October results just the reverse. Temperature laboratory rearings in early summer, 1927, and late fall, 1927, with similar conditions, give nearly identical rates of reproduction.

Factors affecting production of sexual forms may limit their distribution; this will be discussed later.

MIGRATIONS.

The power to migrate is necessary to continued existence when food-plants ripen or die, and is of considerable advantage to the species by keeping the individuals well distributed on favorable plants.

The development of winged females, often termed migrants, is the first step in any extended migration. These are more restless than wingless females, and data at hand indicate that they often leave plants even when nutrition is satisfactory. Seven out of 15 winged

adults used in rearing were missing after producing 3 to 15 young, which was less than half the average for those kept till death. With wingless females only 13 out of 67 were missing so early in the reproduction period. Migrants just arrived were found in the field with small groups of young; a few days later, groups of half-grown young were found without adults, and winged adults with smaller young were seen on nearby plants. Wingless adults and large nymphs usually remain on satisfactory plants throughout life; but they have been observed many times to leave unfavorable plants. The small nymphs leave the plants less readily, and are usually the last to be found on dying plants. The sexes are very restless and difficult to keep caged; their wanderings may be useful in bringing them together, as they have not appeared to recognize each other more than a few millimeters away.

Rhopalosiphum prunifoliæ Fitch, another common grain aphid, has been observed to have a much greater tendency than Toxoptera to leave the food-plants and seek others; it also produces the winged form more quickly under adverse nutrition (Wadley, 1923). *Macrosiphum granarium* Kirby seems to be intermediate in this respect. The greater tendency to concentrate its feeding may be one reason for the economic importance of Toxoptera as compared with these species.

Migration by walking has a limited importance; even winged females have been seen to travel by walking more often than by flight. Plants have become infested in the greenhouse by wingless aphids from sources 3 feet away. The circular infested spots sometimes seen in grain fields are such as would be expected if aphids walked in random directions from a center of infestation. Adults were seen to walk 50 to 75 mm. per minute; small nymphs, 12 mm. per minute. An aphid walking over soil, on seeing an upright object, usually climbs it; it often attempts to feed and may settle down if feeding is satisfactory. When disturbed the tendency is reversed, and the aphid will climb down or even drop from a plant, and will often avoid a plant encountered in walking over soil. After wandering a short time the tendency is again reversed, and the aphid will climb a plant and settle down if there is opportunity. Winged and wingless adults, in the writer's observations, did not respond to sight of a plant over 6 mm. away, and no effect of light on direction of walking was seen. The principal stimulus to leaving seemed to be unsatisfactory nutrition; mechanical disturbance also caused it, and aphids were seen to leave the plants for moist soil when heat became extreme.

Flight seems to require a strong effort, and the winged aphid does not attempt it unless in a good position. Mechanical disturbance may stimulate to flight, especially in warm air. The wind has already been mentioned as a stimulus; the action on the aphid may be direct or through shaking the plants. It has also been noted that flight in still air is not strong, but that it seems to require little effort in a wind; and that the wind governs direction and apparently duration of flight.

Distance covered is difficult to determine. Sanborn (1916) states that *Toxoptera graminum* may spread 50 miles in a day; Webster and Phillips (1912) describing the infestation in 1907, indicate a sudden spread of about 100 miles. *Toxoptera graminum* often occurs in the northern states and Canada in summer, although wintering there has not been found possible. In 1927 migrants appeared suddenly in Minnesota when the nearest known source was about 200 miles away. In 1926 spread must have been much farther. Four winged adults lived without food from 4 to 6 days with the temperature usually 50° and 60° F.; a long flight without feeding would seem possible under cool conditions. Elton (1926) observed live aphids of a Lachnid species flying with the wind to Spitzbergen, the nearest possible source being 800 miles away. Distance covered must depend on the duration of the wind. Migrants of Toxoptera are found in new territory well scattered, with no association with lines of travel, or other evidence of commercial spread.

Swarms of flying Toxoptera have been noted in connection with several outbreaks. Small numbers fly unsuspected by ordinary observers, but revealed by screen studies as with other aphids. There can be no doubt, however, that the species has a greater tendency than many aphids to develop swarms. This can best be ascribed to the extremely severe injury, which causes nutrition to fail and many winged forms to develop at once; also possibly to a uniformity of response to stimuli, which causes many to rise at once. No evidence of communication has been observed. The swarms do not seem to keep together, but are thinly distributed in new territory. It is not known whether individual winged females may make successive long flights, but meager evidence indicates that they do not. The northern states are usually reached in midsummer, several generations later than states just north of the wintering territory; not about the same time, as would be the case if successive flights by the same individual occurred.

It has been noted that Toxoptera was not observed to recognize favorable food-plants at first contact, or to respond to sight of plants more than 6 mm. away. Flying aphids may have better vision, but seem unlikely to discriminate much. These observations seem to stamp migrations as hit-or-miss affairs, often with small chance of success for any given individual. In 1926 swarms developed in Minnesota; a few weeks later the species was hard to find. This reduction cannot be altogether due to the enemies which allowed the swarms to develop, but must be partly due to migration losses. If the aphids were able to seek out food-plants, they would be expected to cluster thickly on the few which are present in late summer; nothing like this occurs. Migrations preserve the species, but must be disastrous to many individuals.

POTENTIAL INCREASE OF POPULATION.

Toxoptera graminum is similar to many aphids in rapidity of potential increase. This is usually held in check by resistance from various sources. Failure or ripening of food-plants, migration losses associated with food scarcity, rain, cold, and insect enemies have been important in Minnesota. The approximate seasonal distribution of these factors is graphed in Fig. 9.

With Toxoptera the number of young is not large for an insect, though all are females; but young are born in a comparatively advanced state, and post-embryonic development occupies only a short time. In computing possible increase, it is found that soon after young mature and begin reproducing, the parent's reproduction becomes only a

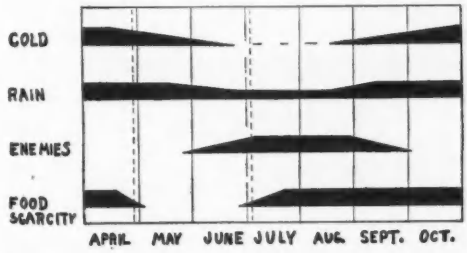


Fig. 9. Seasonal distribution of checks on Toxoptera in Minnesota. Dotted lines inclose part of year most favorable for increase. Combined thickness of blocks at any given time gives an idea of total resistance. (Cold makes development impossible, November to March, inclusive.)

small part of the total daily increase. Hence, time required for development, and reproduction rate early in adult life, are most important in rapid increase. Any factor affecting reproduction and development will affect population growth to a degree which is practically a product of the effects on these two. Temperature has a potent influence. Length of day has an influence, but is not so important in the field, as short days occur mostly when temperatures are low. Food is important, as already shown. Any condition producing many winged forms will decrease reproduction and cause scattering.

The period of reproduction is so long that generations overlap at ordinary temperatures, and calculation of possible increase is complicated. The problem is that of a series of overlapping arithmetical progressions; increasing in number, magnitude, and complexity in relations, in geometrical progression. This can readily be seen by calculating the increase under given conditions for two or three generations; adding the young produced by the daily maturing first and second generation aphids to the continuing reproduction of the parent. It seems impossible to find a formula that will be exact and not too complex for practical use. The best method tried so far to obtain an approxima-

tion of possible increase, is to calculate arithmetically until well into the third generation, when proportion of adults becomes nearly stable; then to calculate further, if desired, by using the daily percentage of increase found in the third generation. Table XIX shows possibilities calculated from approximations of figures from Tables III and IV for constant temperatures. Fractional reproduction is calculated by alternation; for example, with 4¼ young per day, 5 are counted for the first day, 4 per day for the next 3 days, and so on.

In outdoor rearing with the most favorable conditions, reproduction was seldom over 4 young per day, and development required at least 7 days. With these rates, increase would approach that calculated for 22 to 27° C. The percentage of reproducing adults in the third generation, in hypothetical calculations, is about 12%; in several actual cases in rapidly increasing colonies it was between 10 and 15%.

TABLE XIX.

POSSIBLE INCREASE OF TOXOPTERA GRAMINUM, WINGLESS ON OATS, STARTING WITH ONE YOUNG ADULT.

Temperature, °C.	POPULATION AT				Approximate Percent Daily Increase, Third Generation
	5 Days	10 Days	15 Days	20 Days	
12	6	11	16	21	.....
17–17½	13	22	77	251	25
20	16	45	256	904	35
22–23	23	156	807	6,167	50
26–27	21	164	962	7,082	50
30	20	181	1,202	8,501	50
32	9	29	63	319	.....

The increase may also be calculated by number of generations possible, instead of by days. Here the length of development is not a factor, and the measure of increase is the number of young produced before the oldest young mature. This is found to be nearly constant, about 26, over a temperature range from a little over 12° to nearly 30°, except for the favorable temperature about 22°. At the beginning of a generation, young vary from just maturing to newly born; a generation later, the same individuals will vary from some which have reproduced all the time to some just beginning to reproduce; the average will have reproduced about half the period. If 26 young are produced in the minimum time for a generation, the population should increase about 13 times each generation. Examination of several hypothetical series confirms this. The method may be useful in calculating possible increase over a period of varying temperatures.

In several cases one or more females were put into pot-cages containing 4 oat plants of 2 leaves each, and allowed to reproduce unchecked. Reproduction was limited by day-length, as part of this work was done in winter; the theoretical increase was calculated in

each case for reproductive and developmental rates prevailing in the first generation. Production of a few sexual forms interfered very little with the experiments, as they were usually the later-born of the first generation. In most cases the second generation increase held close to the theoretical figure up to a certain point. The plants then

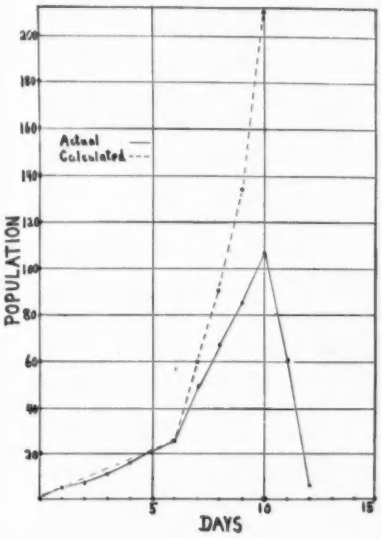


Fig. 10.

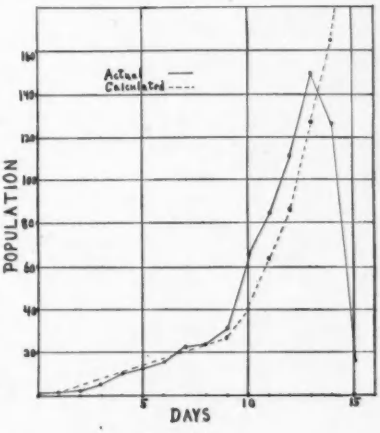


Fig. 11.

Typical case, population increase, *Toxoptera graminum*.

invariably failed and died, and there was a sudden drop in aphid population. All aphids left in 2 to 6 days after the peak in numbers. Seven cases with one parent at the start are presented in Table XX; two are selected to graph in Figures 10 and 11.

TABLE XX.

ACTUAL POPULATION INCREASE.

Maximum Number Aphids	Time to Reach Maximum Days	Calculated Number Reached in Same Period	Calculated Time to Reach Actual Maximum, Days
235	18	484	15
150	13	127	13½
107	11	211	9½
262	21	329	20
61	17	73	16½
102	17	128	16+
101	23	265	18+

As the plants were injured, reproduction was restricted and aphids left. Leaving was observed to begin as long as 4 days before the peak in numbers was reached. In several experiments, parallel tests starting with 2 to 16 females were also run. In general, results were similar to those with one parent, but the maximum came earlier with the greater initial numbers and was usually lower. One case is graphed in Figure 12.

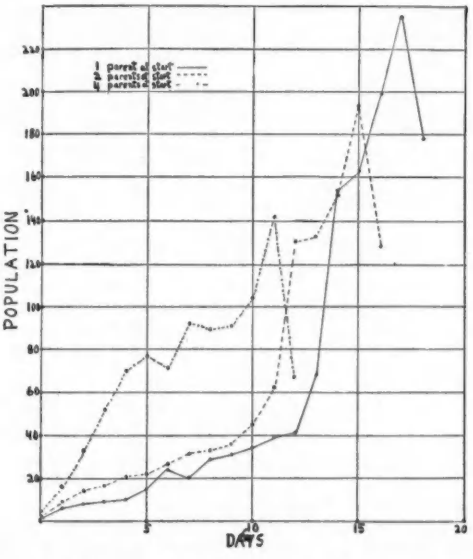


Fig. 12. Typical cases, population increase, *Toxoptera graminum*.

In studying these experiments, it appears that the highest population numbers are reached when many small nymphs are present; plants fail more quickly when large nymphs and adults are numerous. Populations increasing rapidly have been counted in 3 cases; nymphs in the first two instars constituted 60 to 65 per cent, and large nymphs about 25 per cent. As reproduction slows down, the proportion of large nymphs increases; later, as large nymphs and adults leave, the few remaining will be nearly all small nymphs.

Rhopalosiphum prunifoliæ is very like Toxoptera in rapidity of development and reproduction, while *Macrosiphum granarium* is somewhat slower, but generally similar. Their theoretical increase is like that computed for Toxoptera. In several cage experiments like those of Table XX, however, these species gave results quite different from those with Toxoptera. Two typical cases are graphed in Figures 13 and 14. A rough equilibrium was reached in which aphids leaving (sometimes found dead trying to escape), balanced reproduction.

The food-plants survived indefinitely, though stunted by feeding. With Toxoptera death of the plants occurred before aphids leaving could bring about such an equilibrium. This is believed to be because of the characteristic feeding injury of Toxoptera, not shared by the other species, and this injury is probably an important factor in the greater economic importance of Toxoptera.

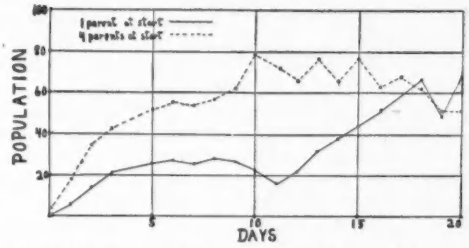


Fig. 13. Typical case, population increase, *Rhopalosiphum prunifoliæ*.

In studying field increase, few figures are available. In 1926, in one locality in Minnesota, *Toxoptera graminum* had reached probably several thousand per square foot in places before the middle of June,

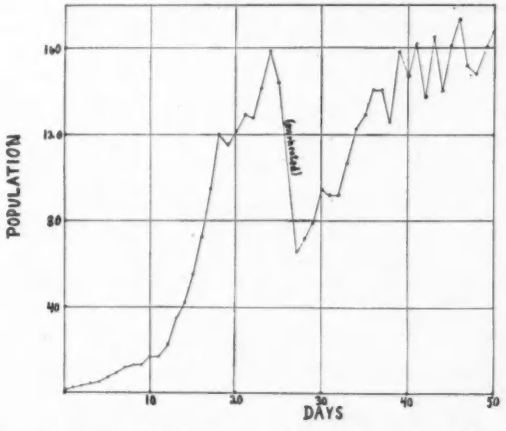


Fig. 14. Population increase, *Macrosiphum granarium*.

on oats which came up late in April. In August, over 4,000 developed in 28 days in an out-door cage from 2 winged adults, at about 70° F. In 1927, a very light but rather uniform infestation of winged *Toxoptera graminum* appeared June 19; in one place 3 were found on 3 square yards. In one field of late wheat, enemies were not abundant and food was favorable. Little rain fell, and the temperature averaged

about 71° F. On July 13 several counts showed 2700 Toxoptera per square yard. Even here potential increase for 22° was not realized (Table XIX). Toxoptera in the field sometimes rises to great numbers when not checked, destroys the food-plants and decreases in numbers suddenly, as in cage experiments.

Two-leaf plants often support 50 *Toxoptera graminum* before failing; on one-leaf plants about 30 have developed. On one large four-leaf oat plant 154 developed. On rather small three-leaf plants in the outdoor cage mentioned, about 4000 Toxoptera developed on 2 square feet. A concentration considerably greater than this was seen in a heavily infested field in 1926. Large leaves may have 50 Toxoptera or more, and on large oats in joint 200 large leaves per square foot may occur. It seems probable that on one- or two-leaf oats Toxoptera may reach nearly 1000 per square foot before killing the plants; on oats of 3 or more leaves, not jointed, 2000 may be reached; and on large oats in joint, as high as 10,000 per square foot might be attained. In the wheat field mentioned, an infestation of 300 per square foot on large plants was not noticeable except on close inspection. All observations indicate that the peak number is much in excess of that which would be required to kill the plants by continuous feeding.

ENEMIES.

Insect enemies are important in holding economic aphids in check, though by no means the only factors checking them. Nearly every writer on *Toxoptera graminum* has discussed enemies. Few references to insects beneficial to the species occur; ants appear interested in Toxoptera, but do not attend it as they do aphids secreting much honey-dew. Parasites of its insect enemies may be considered beneficial to it. Many predators will probably attack *Toxoptera graminum* and other aphids, though they do not concentrate their work as do insects specialized in attacking aphids. Small spiders and large mites have attacked *Toxoptera graminum* in cages, and dragon-flies have been seen around infested grain. McAtee (1913) records observations on birds attacking grain aphids; the numbers eaten would not effectively control heavy infestations. Disease seems to be unimportant with this species; it was not observed even with 100 per cent relative humidity.

In Minnesota, Coccinellids, Syrphids, hymenopterous parasites, Cecidomyiids, and Chrysopids are active in attacking aphids; they are given here in order of importance in connection with *Toxoptera graminum* in 1926 and 1927. Most American workers, dealing with more southern conditions, rank Hymenoptera first; Moore (1914), in Africa, gives Coccinellids high rank.

The test of effectiveness for an enemy of an injurious insect, from man's standpoint, is the power to prevent injury; it involves not only power to reduce the host's numbers, but ability to maintain itself between outbreaks of the host, and to attack it before it is greatly concentrated and doing much injury.

Coccinellids.

Five species of Coccinellids were more or less important in connection with *Toxoptera graminum* in Minnesota: *Coccinella novemnotata* Hbst., *C. transversoguttata* Fald., *Hippodamia convergens* Guer., *M. parenthesis* Say, and *H. tredecimpunctata* L. All frequent low-growing plants. *Adalia bipunctata* L. was numerous; it feeds readily on Toxoptera, but its habitat in trees and shrubs does not bring it in contact with grain aphids. Other Coccinellids were observed only in small numbers during this work. Dr. M. H. Hatch, then with the entomology department, assisted in determining these.

The life-cycles of the species are very similar. They differ in size and in the number of aphids consumed. *C. novemnotata* and *C. transversoguttata* are comparatively large, *H. parenthesis* and *H. tredecimpunctata* are smaller, and *H. convergens* is of intermediate size. Some life history data are recorded in Table XXI; they were worked out in the greenhouse in June and July, temperature averaging about 75° F. Rearing was carried on in vials.

TABLE XXI.

Data on Coccinellid Life History.

Species	No. reared	Egg Stage, Days	Larval Instars, Days Average	Total Days	Aphids Eaten by Instars, Average	Total No. Eaten	Pupal Stage, Days
C. 9-notata....	10	3–4	3, 2, 2.2, 5.8	13.0	27, 33, 56, 258	374	4.8
C. transverso-guttata.....	5	3	2.4, 2.4, 1.8, 5.6	12.2	15, 29, 48, 253	345	5.2
H. convergens.	3	3	3.5, 2.5, 2.3, 7.0	15.3	21, 30, 58, 201	310	4.5

The aphids furnished were *Toxoptera graminum* from stock cages in sizes in proportion as they occurred in growing colonies. (This is true of all feeding tests made with enemies). On single days in the last instar 75 to 100 aphids may be eaten.

Life cycle records for *H. tredecimpunctata* (Cutright, 1924) and *H. parenthesis* (Palmer, 1914) are similar to these. *Megilla maculata* (Tucker, 1918), important in the southwest, and several African Coccinellids (Moore, 1914), also show many similarities. Cutright found that *H. tredecimpunctata* would consume about 120 *Myzus persicæ* in larval life.

Tests showed that the females of *C. novemnotata* and *C. transversoguttata* in summer would readily consume 80 or more Toxoptera daily, and the males about 50. The female of *H. convergens* ate 50 to 75 and the male 30 to 40. A pair of *H. parenthesis* ate 46 in a day. Cutright records that adults of *H. tredecimpunctata* will average 30 *Myzus persicæ* per day.

Table XXII shows some records of oviposition by some reared adults and some collected which appeared to be only beginning oviposition.

TABLE XXII.

OVIPOSITION RECORDS OF COCCINELLIDS.

	Number Females	Date Taken	Average No. Eggs Deposited	Oviposition Period, Days
C. novemnotata.....	4	June 10 to 17	219	4 to 18
C. novemnotata.....	2	Reared	200	36
C. transversoguttata	5	June 1 to 20	167	1 to 25
C. transversoguttata	2	Reared	51	15
H. parenthesis.....	1	July 13	188	47
H. convergens.....	1	June 21	508	14 (escaped)

Coccinella transversoguttata did not thrive in confinement, and the result may not express its full reproductive power. Cutright records an average of about 400 eggs for *H. tredecimpunctata*. Coccinellid females have lived one to two months in confinement. Adults maturing in late summer may live 11 months in Minnesota, judging from field observations. The pre-oviposition period of reared adults was 11 to 14 days. Palmer (1914) and Cutright (1924) record pre-oviposition

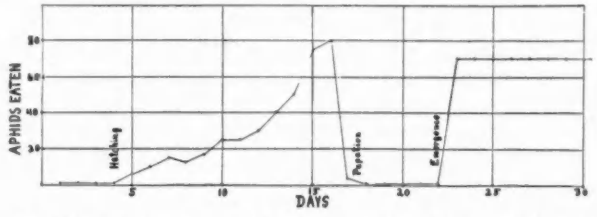


Fig. 15. Life cycle and consumption of Toxoptera, of a typical Coccinellid.

periods of from 1 to 10 days for species treated here. Reared adults of *H. convergens* did not oviposit, though there were evidences of a second generation in the field. Eggs per day usually vary from none to about 60; in one case *H. convergens* produced 130 in a day. All were kept with males and given a plentiful supply of aphids. Vials were used for rearing. Toxoptera was fed when counts were made; on other occasions aphids were collected as convenient. Figure 15 shows graphically life cycle and aphid consumption of a typical Coccinellid.

Life cycles, including pre-oviposition period, thus totaled a little over a month at 75°, which is somewhat higher than Minnesota summer temperatures outdoors. These species should all have time for two generations and a partial third in Minnesota, except *H. convergens*, which started reproduction later in 1927. In the field a second generation seems to develop. Reproduction began late in May, in 1927,

and development was impeded at first by coolness. New adults of the first generation were first noticed early in July, while eggs and small larvæ were seen up to early August. Reproduction was practically stopped in late summer by scarcity of food in both 1926 and 1927, and some time in September it became too cool for reproduction. It is doubtful if a third generation develops in most seasons. *H. convergens* has not been observed in hibernation in Minnesota. Palmer (1917) and others have recorded the adults congregating in large groups, sometimes hundreds, to hibernate. Adults of the other 4 species hibernated scattered in the open fields under grass or any slight shelter. All came through the winter in considerable numbers; the only count made was with *C. novemnotata*, of which 8 were alive and 2 dead in a small area in the spring.

TABLE XXIII.

OVIPOSITION, FEEDING AND TEMPERATURE.

Temperature °C.	Temperature °F.	Egg Stage, *C. 9-notata*, Days	Eggs per Day *C. 9-notata*	TOXOPTERA EATEN PER DAY PER PAIR	
				C. 9-notata	*H. convergens*
26	78.8	3	14	148	100
23	73.4	.....	8	.....	.....
20	68.0	4	3	123	94
17½	63.5	6	1	72	85
14	57.2	11 (part failed)	0	41	69
10	50.0	all died	0	20	17

It was pointed out by Cutright (1924) and others, and was noted in the field and in experiments, that eggs were not produced without an abundant supply of food. A female of *C. novemnotata*, with an average of 80 aphids a day for 7 days, produced 52 eggs; with 60 aphids a day for 6 days, no eggs. With an abundant supply again given, more eggs were deposited. Larvæ restricted as to food required more time for development than normal, and produced smaller pupæ.

It was early noted that feeding was restricted below 70° F. and nearly stopped at 50° F.; that activity was not general in the spring until temperatures were 70° F. or over, for part of the day. Table XXIII shows some results in the temperature laboratory.

Two larvæ of *C. novemnotata* kept at 17½° and 14° C., required 19 and 30 days, respectively, for the last 2 instars, and consumed 567 and 495 aphids in these instars. The former required 10 days for pupal period; the latter showed no development as a pupa in 12 days, requiring as much time after being removed to 26° as if it had just pupated.

C. novemnotata and *H. convergens* were more numerous in the field than the other species. The reasons for this are not apparent in their reproductive rate, but must be sought in some other factors. Resistance to unfavorable conditions, or ability to find food, may be greater with these species.

The Coccinellids rank high as efficient aphid enemies not only because of the high destructive and reproductive powers shown, but because of hardiness, migratory powers, quickness in producing feeding young, ability to attack small numbers, and ability to maintain their numbers between outbreaks. Adults are present in large numbers early in summer because of their ability to hibernate successfully and live a long time without much food; when food becomes plentiful oviposition begins in a few days. A generation matured late in July, 1926, in eastern Minnesota, feeding largely on the green bug. Food was scarce and reproduction was not observed during the rest of the season. When Toxoptera appeared in June, 1927, many were still present and attack on Toxoptera was seen 11 days after the first migrants appeared. They do not, however, find all aphids, especially small groups. The Coccinellids attacked many common aphids in 1927; the cabbage aphid was fed on only sparingly. According to the literature they attack many suitable insect stages; Forbes (1905) records them as feeding on plant material such as pollen and fungus spores. They are thus able to use a variety of food, but when aphids are abundant will apparently leave everything else. Reproduction has not been observed by the writer in these Coccinellid species except when aphids were plentiful.

A hypothetical calculation, using life history and feeding data worked out, shows that two pairs of *C. novemnotata* could wipe out a colony of 1000 Toxoptera in less than a week in summer, while one pair would keep numbers surprisingly low. It seems unlikely that numbers could be kept in equlibrium, because this implies an aphid consumption equal to aphid increase; when the Coccinellids increased further, aphids would be decreased. A sort of equilibrium can occur in practice when aphids are scarce and Coccinellids not reproducing, enough aphids escaping notice to keep small numbers alive.

Several factors have been observed which detract from their efficiency. They are much reduced in activity below 70° F. In May, 1927 (average about 55°), they showed little activity, while native aphids were multiplying in the field. They seem quite likely to attack other aphid enemies, and often leave a few aphids in sheltered places.

Palmer (1914) and Cutright (1924) name several parasites of different stages; these have not been taken in Minnesota so far. The chief natural control of Coccinellids there seems to be repressed reproduction, larval mortality, and cannibalism, when food is scarce.

Syrphids.

Syrphids were well represented in *Toxoptera graminum* infestations in July, 1926, though not as abundant as Coccinellids. Later a few attacked Toxoptera in the greenhouse. In 1927, they were found in the field where *Toxoptera graminum* attained its greatest numbers. Only 3 species were connected with Toxoptera. *Syrphus americana* Wied. and *Allograpta obliqua* Say were numerous all season and attacked many species of aphids; *Sphaerophoria cylindrica* Say was not generally numerous, but several were reared from larvæ feeding on *Toxoptera*

graminum. The adults were readily determined, by comparison with specimens in the University collection determined by Metcalf and Curran. The larvæ were described by Metcalf (1913). Webster and Phillips (1912) record these 3 species, also Eupodes and Baccha, attacking *Toxoptera graminum* in the southwest; Moore (1914) records a Xanthogramma in Africa.

The writer has not been able to obtain eggs in confinement, but has reared in the greenhouse larvæ and a few eggs taken in the field. Three *Syrphus americana* required 8 to 11 days from hatching to pupariation, consuming 440 to 472 Toxoptera; five puparia required 7 to 9 days to yield the adult. Two very small larvæ of Allograpta required 5 days each to complete development and ate 242 and 270 Toxoptera; 10 puparia required 6 to 11 days, averaging 8.3 days to yield the adults. Three Sphaerophoria spent 5 to 6 days as puparia.

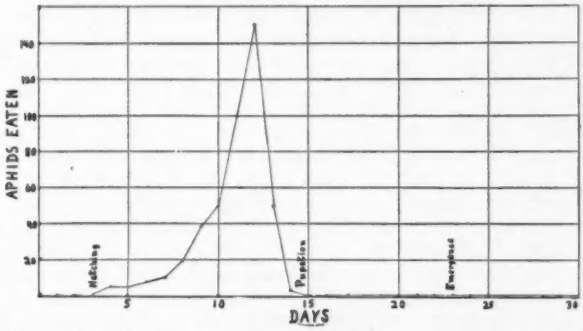


Fig. 16. Life cycle and consumption of Toxoptera, of a typical Syrphid.

Some adults were dissected. One Syrphus had 66 eggs. Six Allograpta had from 16 to 58; three of these had from 54 to 58, indicating a maximum near 60. One new adult of Allograpta had only a few eggs, small and indistinct; this may indicate a pre-oviposition period of adult life in which eggs develop. Adults did not live over 7 days in confinement, even when fed sweetened water. The larvæ reared ate 10 aphids a day, or less, the first few days, then fed and grew rapidly; three-fourths of the total aphid consumption was eaten in 3 days, as high as 150 aphids in a day by Syrphus. The aphids are sucked dry, the skins being left. Figure 16 shows graphically life and aphid consumption of a typical Syrphid.

Metcalf (1913, 1916) records egg stages of 2½ to 3½ days, and larval stages of 8 to 14 days for these species. Adults deposited as high as nearly 100 eggs. He found larval life might be prolonged if food was scarce.

Adult Syrphids hover over plants and seem to examine them carefully. Eggs are usually found on leaves well infested with aphids, and only one or a few on a leaf. The adults seem to require warmth and

sunshine for activity. A decrease in numbers of larvæ, presumably due to less oviposition, followed a cool, cloudy period in August; after a sunny period numbers again increased. Larvæ are not so sensitive to coolness; one of *S. americana*, at the height of its feeding power, ate 94 Toxoptera in a day at 14° C., 35 at 10°.

The first larva occurred early in June, 1927, in a sunny location; larvæ became common late in June. Adults were most abundant in early July and early August; larvæ in late June, late July, and early September. July 25, about half the aphid-infested cabbage leaves in one garden bore Syrphid larvæ; August 31, about one-third; September 8, following two weeks of sunny weather, about two-thirds. Adults were not reared after September 10 at outdoor temperatures; only puparia were present in October. Syrphid larvæ were found late in summer feeding on the cabbage aphid, which was avoided by Coccinellids. Metcalf (1913) believes the puparium to be the hibernating stage.

Of 26 larvæ collected in July and August to rear, 9 yielded parasites. *Bassus laetatorius* Fab. was the principal parasite, occurring one in a host, and emerging 11 to 17 days after the host puparium was formed. One specimen of *B. frontalis* Cress. was reared, from a larva also yielding a *B. laetatorius*. A third species, *Syrphoctonus maculifrons* Cress., was reared from several puparia. Two larvæ yielded small chalcids, 8 or 9 to a host, determined as *Pachyneuron allograptæ* Ashm.

Data given will indicate the power of controlling aphids. The Syrphids do not destroy parasitized aphids; they are able to penetrate pseudogalls and other inclosed places. They feed on a large number of aphid species. Adults seem to show considerable discrimination in finding oviposition places, so that large aphid infestations soon have eggs among them; larvæ will be present and growing within a week later. Hibernation must be fairly successful, as the first generation is numerous.

Only the larvæ feed on aphids, and most of the feeding is during a brief period; however, variations in emergence and adult longevity may give a fairly continuous supply of eggs. Syrphids are often considerably parasitized. In Minnesota in 1927 parasitism was not sufficient to check their attack on aphids; but parasitism has checked them in localities of longer seasons (Metcalf 1913, Moore 1914). The Syrphids appeared rather late in the season, perhaps because coolness prevented adult activity. Their most serious weakness in aphid control, however, is the fact that they seem to attack only where aphids are already numerous. Adults seem to select crowded colonies for oviposition. The larvæ can hardly travel over soil, and probably need plenty of food close at hand; the rather helpless newly hatched larva may require close proximity to food to succeed. Plants with large leaves, such as cabbage, are best adapted for them; oats can hardly support enough aphids for Syrphid larvæ unless crowded.

On the whole, the Syrphids were a definite check on all aphids observed in Minnesota, but were less efficient than the Coccinellids as enemies of most species, mainly because they required a high host concentration before beginning work. They have appeared among

Toxoptera colonies in every case in which the aphids became very numerous, but have not been seen attacking small infestations.

Hymenopterous Parasites.

Webster and Phillips (1912) list a number of parasites reared from *Toxoptera graminum*, both ichneumonoid and chalcidoid; also several chalcidoid and cynipoid secondary parasites. Webster (1914) adds a chalcidoid parasite; Moore (1914) adds another ichneumonoid parasite of considerable efficiency, and notes that *Diaretus rapæ* Curt. will attack Toxoptera sparingly when near the cabbage aphid, its regular host. The currant aphid parasite, *Aphidius ribis* Halid;. and also a species of Monoctonus; may here be added to the list. *Lysiphlebus* (*Aphidius*) *testaceipes* Cresson, an ichneumonoid parasite of the subfamily Aphidiinæ, is recorded in the literature as showing considerable power of control. Aphidius, Monoctonus, and Diaretus are also genera of this subfamily.

Hymenopterous parasites have not been of importance in Minnesota in 1926 and 1927. A few Lysiphlebus were reared from Toxoptera in midsummer, 1926. Late in the season Toxoptera was scarce in the field and no parasites were found. In the greenhouse a few parasitized Toxoptera were seen in late summer, but the parasitism failed to increase. In 1927, *Toxoptera graminum* on open oat beds in the greenhouse showed a slight degree of parasitism late in June. One parasite reared proved to be *Aphidius ribis* Halid., which was attacking the currant aphid outdoors at the same time, and might readily have come in through the ventilators. *Toxoptera graminum* appeared in the field late in June, and by mid-July increased to considerable numbers in spots. In one well infested field, July 12, 0.5 per cent parasitism was shown; in a smaller infestation 5 out of 35 were parasitized, or 14.3 per cent. These parasites, on rearing, proved to be *Lysiphlebus testaceipes*. The rest of the summer Toxoptera was held down by predators, and no parasites were seen in the field. In the greenhouse in August, a few parasites attacked Toxoptera, but failed to increase as before. Some reared included *Aphidius ribis* Halid., *Monoctonus sp.*, *Aphelinus semiflavus* Howard and one specimen of *Pachyneuron siphonophoræ* Ashm. The last named is probably a secondary parasite. To sum up, Lysiphlebus appeared only in small numbers, and after the season and the Toxoptera infestation were well advanced; the infestation decreased from other causes before Lysiphlebus had a chance to increase, and the parasite disappeared. Other parasites attacked Toxoptera, but did not increase on it, apparently failing to thrive.

Some notes may be added on parasitic control of other species of aphids. Most species observed were not parasitized much in the field in 1927. The currant aphid was considerably parasitized by *Aphidius ribis* Halid., the cabbage aphid by *Diaretus rapæ* Curt, in June and later. Both these parasites were themselves checked by secondary chalcidoid and cynipoid parasites in July and later. *Macrosiphum*

granarium Kirby, present only in small numbers, was lightly parasitized by *Aphidius nigripes* Ashm; it has been highly parasitized in Minnesota when numerous (Washburn, 1908-A).

Parasites of aphids and Syrphids were determined from works by Ashmead (1900, 1903, 1904); Gahan (1911); Howard (1908); Hartley (1922); Girault (1917); Viereck (1916). Determinations were kindly confirmed by specialists of the U. S. Bureau of Entomology.

Records of effective control of Toxoptera by Lysiphlebus farther south are many and detailed. Webster and Phillips (1912) give many important facts on the life history of the parasite, showing that it may increase several times as fast as its host at moderate temperatures, but that it is checked by coolness, and inactive below about 56° F. How percentage of parasitism varies with density of host population is an interesting question; it is to be hoped that such records will be made in the future. The writer in Minnesota and Tucker (1918) in Texas found that the parasite practically disappeared when its host became scarce. Other aphid species have been recorded as hosts; these probably carry the parasite over when Toxoptera is scarce. The efficiency of Lysiphlebus in control of Toxoptera will be less than generally supposed if it proves that the parasite requires a high host concentration before beginning work.

Webster and Phillips describe successful hibernation of Lysiphlebus, and activity as early as March or April, in Oklahoma; accounts of numbers developing show that it must be generally present at the opening of the season. In Minnesota it was much slower in beginning work, even considering the later spring there; it has appeared in small numbers only after Toxoptera has been present and temperatures favorable for some weeks, and after related parasites have been active for some time. It is evidently absent or scarce at the beginning of the season in Minnesota, and probably fails to winter or winters only in restricted environments.

Cecidomyiidæ.

Several writers have noted small Cecidomyiid larvæ attacking *Toxoptera graminum*. The writer found and reared two attacking Toxoptera in the greenhouse in late summer of 1926. These larvæ were present in infestations of various aphids in 1927, from July to early September, though they were not found attacking *Toxoptera graminum*. They feed readily on Toxoptera, sucking out their juices. Some have been determined by the use of Felt's treatise on this section of the family (1917), as *Aphidoletes meridionalis* Felt. Davis (1916) found adults to deposit over 100 eggs, and each larva to consume several dozen aphids, and to require about 3 weeks in development in summer. They have not been observed to constitute a major check to any aphid species; factors limiting their efficiency are not yet discovered, except that they evidently multiply only in warm weather. They may be considered a minor check to aphids which become considerably concentrated.

Chrysopidæ.

A few eggs and larvæ of Chrysopids occurred in fields infested with *Toxoptera graminum* in July in both 1926 and 1927; in September, 1926, a larva penetrated a rearing cage. The only adults taken were determined from Bank's key (1903) as *Chrysopa plorabunda; C. oculata* also occurs in Minnesota. Activity has not been noted in Minnesota before July, too late for importance in grain aphid control. The ability of the larvæ to move actively in search of food, and to attack scattered aphids, is of value in late summer aphid control. Smith (1902) states that *C. oculata* may consume 170 aphids in a larval life of 19 days.

Biological Control as a Whole in Minnesota.

Regularly occurring aphid species hatched late in April, 1927, and were able to increase slowly without being attacked by enemies for about a month. In some cases considerable abundance was reached. Late in May and during June, enemies began to work, and migrants to develop and leave. These factors caused declines in June, in spite of more rapid reproduction with warmer weather. Colonies on spring food-plants disappeared in many cases in June. Colonies on summer food-plants appeared in June and increased in July. In most cases these were held well in check by enemies. Coccinellids attacked every species observed but the cabbage aphid; dipterous larvæ, those which formed large colonies; and Hymenoptera, certain species evidently adapted to the parasites.

In studying the 1926 outbreak of *Toxoptera graminum* it is found that in the region first noticed as infested, great numbers were present before the middle of June (Ruggles and Wadley, 1927). This corresponds somewhat to the development of native aphids on spring food-plants; natural enemies would not be expected to check the aphids much. In eastern Minnesota infestation evidently came later; late sown grain was most seriously affected, and large numbers were reached in late June or in July. This is similar to development of native aphids on summer food-plants, and some biological control should occur. Late in July, counts showed 3 to 18 Coccinellids per square yard, mostly large larvæ and pupæ, in infested fields; other enemies were much less numerous. These larvæ must have been the progeny of adults occurring not over one to 5 or 10 square yards, and must have consumed from 1000 to 6000 Toxoptera per square yard in developing. This number is not sufficient to control a severe outbreak; large swarms of migrants developed in some cases. Lack of biological control seemed to be due to small numbers of enemies at the start, so that migrants gave rise to groups of aphids without interference, in many cases.

In 1927, few large infestations of Toxoptera developed. The first migrants came late in June; food-plants became mature soon after this and predators were active. In one late-sown field, counts showed a concentration of 2700 per square yard, approaching injurious numbers.

At this point the plants were reaching an unfavorable stage for Toxoptera. Enemies present included, in areas counted, 5 larval and 7 adult Coccinellids, and 4 Syrphid larvæ, per square yard; and Hymenoptera producing 0.5 per cent parasitism. The Coccinellid adults were just beginning to oviposit, hence were probably recent arrivals. The Coccinellid larvæ were from eggs deposited a week or more before. The predaceous larvæ had probably eaten nearly 1000 aphids per square yard in developing. All predators present could devour about 1000 aphids per square yard per day. As Toxoptera can reproduce at a rate approaching 50% per day in warm weather, numbers would have remained nearly balanced if it had reproduced normally, until more predators developed. On the other hand, if reproduction ceased altogether, due to approaching maturity of the plants, the predators present could wipe out the infestation in 3 days. Actually, all were gone in 8 days; few migrants left the plants.

It is evident that little can be expected from Hymenoptera in controlling Toxoptera in Minnesota; but that predators, especially Coccinellids, will be of considerable value. It is also evident that they must be present in some numbers early in the season to check injury, and that such numbers will depend on food supply the previous season. Infestations of various aphids will keep alive biological resistance which will be of value against injurious aphids. In 1926 they were not able to control *Toxoptera graminum*, even in many eastern Minnesota fields where infestation developed in midsummer. In 1927 they were able to control it, probably because of numbers built up the previous year.

Part II.

Factors Affecting Distribution, Especially as to Northern Outbreaks.

The distribution and importance of *Toxoptera graminum* is obviously much influenced by climate, and by factors such as abundance of food-plants which are themselves affected by climate. Winter cold seems important in connection with distribution, as does rainfall; summer weather and conditions accompanying it have profound effects on numbers of Toxoptera.

DISTRIBUTION RECORDS.

From a study of the literature Toxoptera may be said in general to be important only in the lower temperate latitudes where grain growing is widespread; in higher latitudes it is found temporarily or in small numbers, in the tropics only at high altitudes. The grain areas of South America and Australia, though in lower temperate latitudes, have not been reported as infested.

In America the species has been recorded from most of the states and several Canadian provinces, but seems to occur temporarily or

persist only in small numbers in the north, and to be established in the south. Webster and Phillips (1912) give reasons for believing the species introduced in America, and note the first occurrence in Virginia in 1882, and injury as far west as Texas in 1890. These and other writers (Morrill, 1913; Bentley, 1914; Kelly, 1917; Garman, 1926; U. S. Entomologists' Reports; Insect Pest Survey) give an economic history of the species.

From 1890 to 1927, more or less injury has been done in 16 years; references in other years seem to indicate merely the presence of the species. Injury has been estimated in millions, and has been of major importance to the areas concerned, in 5 years; in 1890 in parts of Texas, Missouri and Illinois; in 1901 northern Texas; in 1907 in Texas, Oklahoma and Kansas; in 1916 in Oklahoma, Kansas and New Mexico; and in 1926 in parts of Minnesota. Infestation was wide spread in some of these years, but the areas named were the ones badly damaged. Injury has been reported several times in the Carolinas and neighboring states, and was rather severe there in 1907.

This study reveals Oklahoma and northern Texas as most frequently injured, a large part of the country east of the Rockies south of 40° latitude as occasionally damaged, and only infrequent injury in other parts of the country.

TABLE XXIV.

TERRITORIAL DISTRIBUTION OF RECORDED INJURY, 1890 TO 1927.

Area	Years of Injury	Years of Major Losses in Parts
N. Texas to Kansas	12	4
States west of this longitude	4	1
States east of this longitude	9	2
Arizona to Carolinas	14	4
States in latitude of Missouri	7	1
States north of this	2	1
Gulf Coast (S. Texas to Georgia)	1	0

INFLUENCE OF RAINFALL ON DISTRIBUTION.

Several writers have shown association of outbreaks of Toxoptera in the region most often infested, with preceding summer rainfall which maintained food-plants, with mild winters, and with late spring. There is also an association of injury with light rainfall, which may be briefly studied here, since it has received little previous attention.

Reduction of numbers of *Toxoptera graminum* by rain has been described. It is obvious that frequent rains will check, but will not eliminate the species; and that if it is generally distributed, a few weeks with little rain will suffice to build up injurious numbers. It is also plain that increase to injurious numbers will take place only when temperatures are high enough for development and crops affected are

immature. This points to the period of injurious increase as late fall, winter and early spring in the south, spring months in the middle states, and late spring and early summer as far north as Minnesota. A third consideration is that the species cannot thrive without sufficient rain to maintain some food-plants through the year. These facts give a basis for examining the influence of rainfall on distribution.

It has been shown that Texas and Oklahoma have had more records of injury than the wide expanse of states to the east, and many more than states farther west. The climate in the states west of Oklahoma is very dry and grain growing is limited. Toxoptera probably has difficulty in maintaining itself through the year because of a precarious food supply associated with very dry conditions. The rainfall of states in the longitude of Oklahoma is sufficient for grain farming, and is heaviest in late spring and summer, and light in fall and winter. Farther east rainfall is somewhat heavier, especially in winter and spring, the time injurious increase must occur in this latitude.

Northern Texas and Oklahoma may be compared with Tennessee and the Carolinas, where Toxoptera has often been reported, but where injury has been less frequent and severe. In the western area, representative weather stations, from November to April, inclusive, average 1½ to 2½ inches of rainfall per month, and from 4 to 7 rainy days per month. In eastern area averages are 3 to 4½ inches and 8 to 12 rainy days, respectively. It seems likely the frequent rains in the east are a factor in repressing Toxoptera; this may be further tested by a study of weather of outbreak years.

It is found that in Texas, Oklahoma and Kansas winter and spring rainfall in the four serious outbreak years has been either about normal or below normal; never much above normal. In the regions east of this longitude, great abundance has usually been associated with deficient rainfall. The 1890 outbreak was serious in parts of Missouri and Illinois near St. Louis, in May and June. It was accompanied by variable and generally deficient rainfall over this area in these months, though winter and early spring had been rainy. The conditions were similar in the 1926 outbreak in Minnesota and neighboring states, as will be more fully discussed later. The 1907 outbreak in Virginia and the Carolinas followed a winter of marked deficiency in moisture, with some very dry months. The less marked outbreaks in South Carolina in 1913, and in South Carolina and northern Georgia in 1914, are found to be associated with some deficiency in winter rainfall; in the former year Luginbill (1914) speaks of March rains helping to end the outbreak. A number of complaints in Tennessee in the spring of 1913 were associated with a dry April. The less important occurrences are harder to relate to weather, especially as the exact localities infested are often not recorded.

In 1915 the green bug was widely distributed in fall and early winter over Oklahoma, southern Kansas, northern Texas and northeastern New Mexico, (Webster, 1916). However, very heavy rains fell in January and again in April, in northern Texas and southern Oklahoma, and damage seems not to have developed there. In southern Kansas,

northern Oklahoma, and New Mexico it remained dry, and injury was severe (Kelly, 1917).

It is concluded that the green bug is most often injurious in a region having rainfall that is sufficient for grain production, but is rather light, with comparatively long dry spells, during the period of injurious increase. In rainier areas injury is less frequent and is usually associated with rainfall shortage. It seems likely that this relation may be

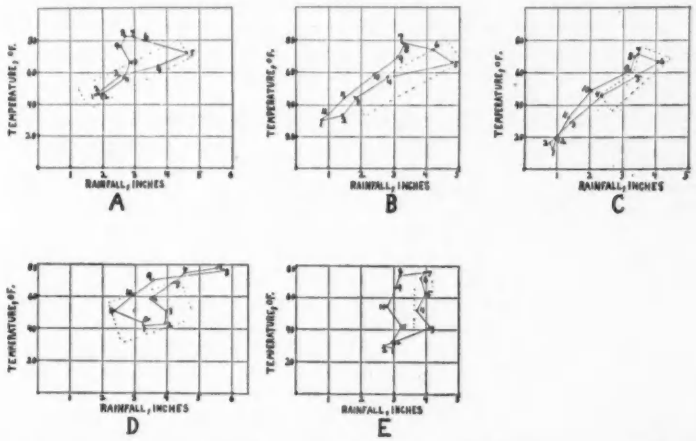


Fig. 17. Climographs of monthly means, localities of interest with respect to *Toxoptera graminum*. Broken lines inclose parts of year in which injurious increase occurs.

A. Fort Worth Texas. Winter temperatures and rainfall favorable.
B. Wichita, Kansas. Winter temperatures less favorable, rainfall favorable.
C. St. Paul, Minnesota. Winter temperatures very unfavorable, spring rainfall not very favorable.
D. Raleigh, North Carolina. Winter temperatures favorable, rainfall less favorable.
E. Indianapolis, Indiana. Neither winter temperatures nor rainfall very favorable.

ascribed to the known action of rain in reducing numbers. The foreign distribution of recorded injury (Hungary, Italy, southern Russia, South Africa) agrees in general with this conclusion. Minnesota is not particularly favorable from the standpoint of rainfall; injurious increase must take place in May and June, which normally have from 3 to 5 inches of rain and 8 to 11 rainy days, at most weather stations.

Climographs of several representative localities, of interest with respect to Toxoptera, are shown in figure 17.

EFFECT OF SUMMER CONDITIONS.

The problem of surviving the summer is a serious one for this species. A great reduction in numbers takes place; it cannot be explained by direct effects of heat in the northern states. The most apparent causes are food scarcity and associated migration losses, as grain crops mature, and increased activity of enemies. In the south these conditions may be expected to be worse and more prolonged, with added injurious effects of high temperatures; summer conditions and scarcity of grain crops probably limit distribution southward. Food supply in summer seems to be a critical point; enemies will not exterminate the green bug in the presence of abundant food, judging from observations made in this work.

In Minnesota in 1926 and 1927, Toxoptera persisted in very small numbers through late summer and fall, on volunteer plants of oats and wheat. They were most readily found in thick growths around elevators, which afforded a constant food supply and some shelter from Coccinellids, but a few were observed in the open.

Nothing has been found to indicate that migrants from the north restock the south in the fall, though we have considerable evidence for the reverse happening in the spring. The small and scattered colonies found in the north in the fall would not give rise to many migrants, such as come from southern grain fields in the spring. Toxoptera is sometimes more abundant in late fall in southern states than in territory just north of them, according to Kelly (1917) and the writer's observations, which would not be expected if the sources of infestation were northward. It seems likely that aphids found in the south in winter are descendants of some which survived the summer in that region; and that green bugs which succeed in passing the summer there are the source of much of the injury for the whole country. The question of summer survival in the south is thus of considerable importance; our information upon it is still quite limited.

Though the species has not often been followed through the summer in middle and southern states, its success in going through is attested by numerous records of its presence in fall and winter. Volunteer grain is undoubtedly important in survival there, as in Minnesota; Webster and Phillips (1912) record bluegrass as a summer food resource. Orchard grass occurs in the border states, and Johnson grass farther south; both have been recorded as rather acceptable food. Johnson grass is of especial interest, because of Moore's account (1914) of its importance as a food-plant in South African summers, and because of its flourishing growth under hot, dry conditions. In the area from North Texas to Kansas, most frequently injured, summer conditions are very severe and food supply must be especially critical. Some of the greatest outbreaks have been associated with abundance of volunteer grain the summer and fall before.

Several workers have shown association of injury with late, cool springs; these may be looked upon as seasons in which unfavorable summer conditions are delayed, giving more time for increase to injurious

numbers. Glenn (1909) and Kelly (1917) have shown association of outbreaks with preceding rainy summers, which would maintain food-plants and make summer survival easier.

LIMITATIONS DUE TO WINTER COLD.

Toxoptera graminum is not limited in northern distribution by summer coolness, as suggested by Merriam (1895); the species thrives at summer temperatures in the northern grain-growing regions. It is rather limited by winter cold, as indicated by Sanderson (1908). Toxoptera may appear in spring or summer in spite of winter cold, in three ways. Active aphids or eggs may winter, or migrants from more southern regions may come in.

WINTER EGGS.

Several factors limit the economic status of Toxoptera wintering as eggs. The egg-producing forms may not develop; eggs when produced may not winter successfully; migrants produced by aphids hatching from winter eggs may not reach the grain fields in time to be injurious.

In this work sexual forms have developed after 2 generations under day-length somewhat shorter than 12 hours and temperatures averaging 70° F. or less, and their development has been limited by cold. In both 1926 and 1927 sexual forms began to mature in the greenhouse about October 20, among progeny of parents born after September 25. Day-length evidently became favorable the last week in September of each year. In the outdoor insectary each year only one generation was born and matured, after September 25 and before cold weather; some brought into the greenhouse in November, 1927, produced sexes in the next generation. No sexes were found in small groups observed in the field. In 1926, in a protected outdoor cage, no mature sexes were found in frequent observations, through the fall; but one oviparous female, nearly mature, was seen November 13, just before permanent freezing weather. In 1907, experience in Minnesota was similar to the writer's (Washburn, 1908-A), but some eggs were found in a river gorge the next spring (Washburn, 1908-B). This is a peculiar location; deep gulches may shorten the day by shadows, and give some protection against cold. No Toxoptera were found in such places in 1927.

It is evident that general production of sexual forms of Toxoptera in the field in Minnesota does not occur because of cold stopping development. Such production would require two generations maturing after September. October is nearly always too cold for this to occur, and November allows practically no development, even in the milder falls. In Indiana sexual forms have often occurred (Webster, 1892; Webster and Phillips); the fall is milder than in Minnesota and days shorten nearly as fast. In Kansas, with similar day-length and temperature, but more clear weather than Indiana, sexes were not found in the field in 1907 or 1915, but were seen in 1908 (Kelly). In the south days shorten more slowly, but temperatures even in winter allow some development; it would seem that sexes might occur late in the fall.

They have been seen in the field in Tennessee in 1908 (Webster and Phillips), and reared in South Carolina (Luginbill and Beyer) and, in Texas (Tucker). Published records are too few to furnish a basis for comparison; it seems, however, that these forms occur more commonly in the southern and middle states than in Minnesota, which would be expected from day-length and temperature relations.

As to successful wintering of eggs, data already cited indicate that the eggs are hardly able to withstand Minnesota winters, but that some may come through. It seems that eggs winter successfully in Indiana.

Late development of migrants is a factor limiting economic importance of Toxoptera wintering in the egg. The first generation from the egg, the stem-mothers, develop slowly because of coolness and are wingless. Their progeny must also mature before there is a possibility of migrants leaving winter food-plants. In records of rearing in Indiana, cited by Webster and Phillips (1912), a representative stem-mother hatched March 28, and matured April 18; her oldest progeny matured May 9. In Minnesota most native aphids hatch late in April, and migrants begin to appear about June 1. It seems unlikely that *Toxoptera graminum* wintering as eggs could reach spring grain fields there much before June (see Table II) which is too late to do much damage. It is evident that Toxoptera hatching from winter eggs will hardly be able to injure spring grain, unless very backward weather holds crops back after warm weather has enabled migrants to develop, or unless very late fields occur. Webster and Phillips express doubt as to the importance of such wintering. All important outbreaks on which data are available can be connected with live aphids wintering, or migrants coming in.

It is observed that many aphid species common in Minnesota produce the sexes and eggs in advance of cold weather, and hatch in the spring, quite regularly, in contrast to *Toxoptera graminum*. By day-length relations differing from those of Toxoptera, or some other factors, they are definitely adapted to persist in the north.

Survival of Active Aphids.

Observations on effects of cold on *Toxoptera graminum* have been recorded. They indicate that the aphids can survive cold seasons where minima are somewhat above 0° F. and temperatures are often high enough to permit some development. This survival cannot be called hibernation, but is rather a period of slow development, interrupted by inactivity caused by cold. Aphids found in the spring will probably not be the ones present the fall before, but their descendants, as adults have not been observed to live long enough to pass a winter. With protection, more cold may be withstood; the effect of snow has been mentioned, and the protection of clumps of volunteer grain may approach that recorded by Headlee and McColloch (1913) for prairie grass. Cold prolonged enough to force inactivity for several weeks, however, will be fatal even if not very severe.

Many references are found to survival in the south, especially in the Carolinas, Tennessee, Oklahoma, and Texas. In these states the

normal mean temperatures in winter months are nearly 40° F., or higher, and minima seldom approach 0° F. Data recorded by Webster and Phillips (1912), Hunter (1909), Kelly (1917), and Howard (1921) show that survival may also occur as far north as Kansas and Indiana, at least in the milder winters, but this seems to be less frequent. No records are found of survival in states father north. Records examined do not show widespread survival of months averaging as low as 30° F., and considerable reduction in numbers usually accompanied months below 35° F.

Winter survival by active aphids is of great economic importance. From Table XXIV it will be seen that by far the most frequent injury has been noted in the territory where survival is common. During the milder winters not only survival, but considerable increase and injury may occur; Webster and Phillips, and Glenn (1909) have shown an association of injury with mild winters. Winter oats and wheat, and volunteer grain, are affected. Spring sown grain is reached by migration later. In areas just north of this, where survival is less common, some recorded cases of injury can be ascribed to Toxoptera surviving mild winters. This is true of injury in eastern Kansas in 1908 and 1921. The injury in southern Kansas in 1916 seemed to be worst where aphids survived locally. In this year injury occurred in spite of a rather cold winter, because of large numbers in the fall, and a spring favorable to survivors. In Missouri and Illinois in 1890, the preceding winter was mild enough to have permitted survival; Toxoptera was observed to survive in Indiana, (Webster and Phillips). However, in these latter two cases some indications of infestation by migrants exist. Aphids surviving in the south are a source of infestation by migration for areas farther north.

No indication of possibility of winter survival of this kind in Minnesota can be found. The winter months normally average between 10° and 20° F., and temperatures forcing inactivity may last for months. Minima are often —20° F. or lower, but these seem less important, because of snow protection, than the protracted cold. Records in the literature, field observations, and extensive laboratory experiments do not show sufficient resistance to cold; no records of survival even as far north as Nebraska and Iowa have been found. In 1926, in a fall and early winter not unusually cold at St. Paul, unprotected Toxoptera failed to live through November, and some considerably protected did not survive December outdoors; some observed in the field failed to live through the winter. From all standpoints survival seems impossible, in even the mildest Minnesota winter.

Climographs of several localities of interest with respect to winter survival of Toxoptera are shown in Figure 17.

Spring or Summer Migration to Northern States.

The manner of migration has been discussed. Factors affecting its economic importance may be studied briefly. Records in the literature show that winged forms may leave wintering places in the south as early as March in some years. They probably leave as late as May,

or until grain in the south is nearly mature. They are dependent on the wind; if they drift north, they will reach areas where the season is not so far advanced as in the places they left, and where food supply may be more favorable. If they drift in other directions they will

Fig. 18. Wind direction April 26, 1926. Copied from daily weather map, U. S. Weather Bureau.

Fig. 19. Wind conditions, June 18, 1927. Copied from daily weather map.

reach areas with the season as far advanced as the one they left. In the territory most infested, the wind is often from the south in spring, and a south wind is probably warmer and more stimulating to flight than one from another direction.

Losses and scattering in flight, already mentioned, cut down the number of winged aphids arriving in a given area. If summer conditions are delayed after their arrival, allowing time for several generations without much hindrance, they may be able to rise to injurious numbers in the new area despite this loss and scattering. This delay might conceivably be because of an abnormal season, because of early migration, or because of migration to regions unusually far north where the season is not far advanced.

It seems unlikely that Toxoptera could rise to generally injurious numbers in Minnesota and the Dakotas unless migrants arrived in the fields in April or May, and the most favorable time would be between April 15 and May 15. Before April 15 weather is cold and food is scarce; in June, and even late in May, grain is growing rapidly, and summer conditions are approaching. Migrants arriving in June may give rise to colonies which persist until July, and rather large numbers may be reached in late sown fields, but general injurious increase seems much less likely than if they came earlier.

A week seldom passes in spring in this longitude without south winds, suitable to distribute Toxoptera from a given location to adjoining states. South winds capable of carrying migrants from Texas or Oklahoma to the Canadian border at one time are much less frequent; a "low" or "high" is usually between. The more frequent condition is shown in Figures 18 and 19; the less frequent condition with south wind all the way from Oklahoma to the north, in Figures 20 and 21. The latter condition is associated with a slow-moving "low" in southern Canada. The wind velocity is usually from 200 to 600 miles a day in these periods; a single day's wind would not suffice to bring aphids 700 miles or more from Oklahoma to Minnesota. A study of winds at this time of year, from the U. S. Weather Bureau's Daily Map, is shown below. The periods of wind between April 15 and May 15, which had sufficient wind velocity to distribute green bugs to the north, are also shown separately. Southeast winds are not included; they do not pass over such large areas of winter grain.

TABLE XXV.

FREQUENCY OF PERIODS OF UNIFORM SOUTH OR SOUTHWEST WIND, FROM TEXAS-OKLAHOMA REGION TO MINNESOTA AND DAKOTAS, APRIL AND MAY.

Year	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927
All Periods:										
1-day periods.....	2	1	0	5	2	1	0	2	2	4
2-day periods.....	1	0	0	2	1	0	1	2	2	0
3-day periods.....	1	0	0	0	0	0	0	0	2	0
3-day periods.....	0	0	0	0	0	0	0	0	0	0
Periods favorable as to date and velocity:										
2-day.....	0	0	0	0	0	0	1	0	1	0
3-day.....	0	0	0	0	0	0	0	0	1	0

Wind mileage at different stations for the two most favorable periods in 1926 is shown in Figures 20 and 21; this was kindly furnished by Weather Bureau officials.

Field notes on migration into Minnesota may be mentioned here. In 1927, a careful search was made by the writer in all sorts of favorable locations in Minnesota, but *Toxoptera graminum* could not be found in the spring. On June 19 a few winged forms were found at St. Paul; in the next few days migrants and small young were found at several points around St. Paul, at Winona and at Owatonna. In each place the infestation was of about the same date and of a similar thin distribution. In a plat of late oats the smallness of plants permitted a count; 3 migrants were found on 3 square yards. About the same time

Fig. 20. Wind conditions, April 20, 1926. A representation of conditions both April 19 and 20, with total wind mileage for period shown by each station in probable path of infestation. From Weather Bureau records.

specimens (including nymphs) of *Toxoptera graminum* were received from southeastern Iowa, showing that they were breeding there. The wind June 18 and 19 was suitable to distribute aphids from this region to Minnesota. These facts strongly indicate migration. Toxoptera was found breeding in northwestern Minnesota later in the summer.

In 1925, a winged specimen of *Toxoptera graminum* was taken on a sticky screen in July, at St. Paul, and preserved, by Mr. R. E. Wall. In 1926, an outbreak of Toxoptera occurred in Minnesota, the source probably being early migration; this will be treated more fully under the next heading. In 1928, as the work was being concluded, a few migrants of Toxoptera were found early in May at St. Paul, after several days of south wind. No local source for the migration could be found. Numbers were very small and distribution was not general; most of the small grain was not yet up, owing to unusual cold and snow in April and backwardness of farm work; and a serious infestation did not

develop. In 1907, close search was made for Toxoptera in Minnesota because of reports of injury farther south; none were found until early in July (Washburn, 1908-A). In 1908, some were found in late summer (Washburn, 1908-B).

These records show the presence of Toxoptera in Minnesota in six summers; these are the only years in which it has been looked for as far as can be found. It was reported from neighboring states in 1926; Webster and Phillips (1912) record it from several northern states, Manitoba and Saskatchewan, in 1907. Dr. W. C. Cook has told the writer of records from Montana in several summers; Prof. A. L. Seamans told of frequent occurrence in Alberta in late summer. Thus it has been frequently found in the north, usually in midsummer or later. In several years in Kansas, the writer did not observe Toxoptera

Fig. 21. Wind conditions, May 6, 1926. Representative of conditions May 5 to 7. Total wind mileage for period, by each station in probable path of infestation. From Weather Bureau records.

in early spring; the species appeared in April or May. The late Professor McColloch told the writer the situation was the same there in 1927.

It seems likely that northern states are often, perhaps annually, infested by Toxoptera migrants. Because infestations usually develop in late spring in Kansas, and considerably later in the north; and because the wind is not often suitable to distribute aphids from wintering places to northern states at one flight; it is believed that migration is usually by successive stages. In infestations developing in the middle states, migrants are produced which go farther north. However, in some years migrants may reach the northernmost states by a single migration from places where the winter is passed. Evidence indicates such migration in 1926 and 1928, and suitable winds occur every few years.

Migration has sometimes, but not often, been the source of serious injury; the majority of outbreaks have occurred where the species survives the winter. In 1907, Webster and Phillips leave no doubt that severe injury was done in Kansas by an infestation established by migrants; this was associated with warm weather in early spring and early migration, and with backward weather in late spring, giving time for increase. In 1890 near St. Louis, and in 1916 in Kansas, spring oats were most injured; these must be reached by at least a short migration. In 1916 injury seemed to extend north of the region of general survival. Some injury to oats caused by migrants occurred in Central Kansas in 1922. In 1926 in Minnesota injury seems to be associated with unusually early arrival of migrants. Information given by Prof. C. J. Drake as to conditions in northern Iowa, and observations by the writer in Minnesota, in 1927, causes suspicion that very late-sown spring wheat and oats are slightly injured in the north more often than is generally realized.

PROBABLE SOURCES AND SPREAD OF 1926 OUTBREAK.

We may now inquire as to the causes of the 1926 northern outbreak of Toxoptera, which was in an advanced stage before it was observed. It has been noted by Ainslie (1926) and described by Ruggles and Wadley (1927). Severe injury occurred in western Minnesota; it was noticed first and was especially severe in an area in northern Kandiyohi and adjacent counties. In eastern Minnesota a considerable infestation with some injury occurred. Three possible sources of infestation are local winter survival of active aphids, local wintering of eggs, and migration from farther south.

Survival of active aphids in the field has been shown to be impossible in Minnesota. The winter of 1925-26 was somewhat above normal, but not mild enough for Toxoptera to live through. The three-month period averaged about 20° F. in the southern half, with December and January below 20° F. There seems to be no chance that such survival could have occurred.

Production of sexual forms and eggs by Toxoptera in Minnesota has been shown to be uncommon. The fall of 1925 was even less favorable for their development than usual, owing to general cold weather in October. At New London, in Kandiyohi County mean temperature for October was 38° F., with a minimum of 6°. November was too cold for development. Even aphid species regularly wintering as eggs were reduced in numbers by these conditions, and were scarce the next spring, according to students of the group in Minnesota. The doubt that eggs endure Minnesota winters well has been pointed out. Delay in reaching summer food-plants by aphids wintering as eggs is a third and very serious difficulty in connecting this outbreak with such wintering. In the area most affected, aphids were very numerous before June 15; in some cases large oats in joint were being destroyed, and the aphids must have reached several thousand per square foot. March and the first half of April were too cold for Toxo-

ptera's development at New London and spring grain was not up. In the latter half of April, averaging about 50° F.; May, averaging 60° F.; and the first half of June, averaging 63° F.; about 4 generations of Toxoptera might develop. If they originated from winter eggs, the first two generations must have developed on some winter food-plant, only about two on spring grain. Estimating a possible increase of 13 times per generation, and 45,000 per square yard as maximum population; if four generations developed on oats the minimum initial infestation required would be $\frac{45{,}000}{13^4}$, or less than 2 per square yard; but if only two generations developed on oats, over 250 per square yard would be required. It is very doubtful if development of such numbers as the latter on grasses, and migration to grain, could take place without attracting attention. These approximations show the difficulty of believing such an outbreak to be due to wintering of eggs. Great concentration of Toxoptera occurred on oats not many days after aphid migrants would have been leaving winter food-plants.

As survival of active aphids was impossible, and infestation from winter eggs very improbable, there remains the possibility of migration. Conditions exist which makes this seem probable. Kansas entomologists did not observe Toxoptera in early spring, 1926, but Prof. C. E. Sanborn told the writer of infestations in central Oklahoma in winter and early spring. This was the nearest known infestation to western Minnesota. The occurrence of unusually favorable winds in 1926 has already been recorded (Table XXV, Figs. 20 and 21). In their dates, direction, and distance they would be fitted for the migration needed to explain the Minnesota infestation. About four generations could develop from the windy period of April 19-20 to June 15; something over three generations from May 5-7 to June 15. The initial infestation required would thus be little higher than that observed in 1927.

The wind would be expected to deposit migrants over a wide area. The area in which great numbers were first noticed covered parts of three counties. However, in other counties in that part of Minnesota injury was considerable and large numbers were reached almost as early. Professor Drake told the writer of one infestation in western Iowa. Mr. Nelson of Brooten, Minnesota, who became familiar with the green bug during the outbreak there, described similar infestation and injury near Jamestown, North Dakota, late in June. Some reports were made of Toxoptera, in South Dakota (Insect Pest Survey); Mr. McFadden, of Webster, South Dakota, described injury to oats similar to work of Toxoptera. A number of counties in western Minnesota show large decreases in oat yield not explained by barley yields (see Ruggles and Wadley). A considerable infestation may exist without being observed by farmers. It seems likely that the original infestation was wide-spread in western Minnesota and eastern Dakotas, and perhaps in northwestern Iowa. Farther south the earlier onset of summer would be expected to prevent great increase following infestation.

The rainfall was variable and somewhat deficient in western Minnesota and neighboring states in April, May and early June, with rather long rainless periods. In the area most injured it was especially dry; May had only 1.15 inches of rain, and only two rains of over one-fourth inch fell from April 15 to June 12. This condition undoubtedly favored increase. It seems unlikely that enemies were very active at the temperatures prevailing. Large numbers were reached and migrants left from the middle of June to early July in western Minnesota.

In the eastern Minnesota infestations, the source seems less likely to have been migrants from the south. Large numbers were not reported until July; only late-sown grain was much injured. It seems certain

Fig. 22. Wind conditions, June 22, 1926. From daily weather map.

that infestation came later here. This may also be true of some late infestations in extreme northern Minnesota. At Duluth, oats not up before June 10 at the state experiment farm were infested by June 20; at St. Paul, Toxoptera were seen June 22. Development of Coccinellid larvæ indicated aphid abundance beginning about July 1. Dr. Fracker told the writer of general infestation in Wisconsin, with injurious numbers reached at several points; the Insect Pest Survey reported scattered infestations in Michigan, northern Ohio, and northern Indiana. In these states the largest numbers occurred in July. A southwest wind April 29 and 30 had a total mileage, at several points in its path, of 400 to 700 miles, averaging 560; this would not be sufficient to bring aphids the 700 or more miles from Oklahoma to Wisconsin. The south winds noted seemed less likely to cause this infestation because a large acreage of winter grain was not present directly south of this area.

Migrants were leaving in swarms in the most heavily infested western area by the middle of June, and probably before in smaller

numbers; they were migrating somewhat later from neighboring areas, and some must have been flying nearly all through June. Strong west winds blew in the Dakotas and Lake States on June 6-8, 17-18, and 22-23 (see Fig. 22). Balloons released in grain rust studies in Minnesota were recovered as far away as Ohio. With migrants abundant in western Minnesota, and winds blowing that were capable of carrying them hundreds of miles, infestation of eastern Minnesota and Wisconsin and possibly of spots farther east, is readily accounted for. Rainfall was variable and somewhat short in this region, during much of this time of increase. Enemies attacked the aphids, but did not seem abundant enough to control them.

The infestation varied considerably over the territory. This could result from variable conditions affecting increase as well as from variation in original infestation. The most noticeably variable factor affecting increase was rainfall. Ruggles and Wadley show that dates of reports of large numbers when mapped show a roughly concentric succession around the area most injured. This can hardly be due to successive migrations, since the winged forms produce nearly all wingless progeny, and migrations must thus be at least two generations apart. It is believed that in the small area first injured, large numbers developed earliest because of the local rainfall shortage; around it the greatest numbers came somewhat later; they were probably later farther north because of lower temperatures, and farther south because of more rain in June. In the territory farther east, infested by migrants from this territory, large numbers of course developed still later, again with local variations. It is believed that the concentric appearance is best explained by these differences.

The outbreak may largely be explained by earliness of infestation in the west, conditions favoring migration eastward, light rainfall, and scarcity of enemies. Temperatures of spring and summer are of little help in explaining it. March, April and July temperatures in Minnesota were nearly normal; it was too cold for Toxoptera's development before the middle of April. May was about 5° F. above normal, June about 3° below; these temperatures were somewhat favorable, as Toxoptera could be active over a considerable period when its enemies were checked by cold. Even with normal temperatures, however, considerable increase could have occurred.

It is believed that migrants from the southwest arrived in April or early May and gave rise to widespread and variable infestation in western Minnesota and eastern Dakotas; that migrants from this territory in June infested areas farther east.

PROBABILITY OF NORTHERN OUTBREAKS.

It seems likely that *Toxoptera graminum* will seldom be generally injurious in Minnesota. It is not adapted to wintering there; the winter eggs may enable it to winter somewhat farther north than active aphids can survive, but are not efficient as a hibernating stage in Minnesota.

It does establish itself in the northern states by migration, usually too late to be very injurious except perhaps to very late grain. It has been as far west as Texas at least since 1890, and has only once been seriously injurious in the north. It can be seen that the 1926 outbreak was due to several favorable circumstances occurring together; including winds suitable for a long migration early in the season, migrants on the wing at the time the winds blew, and dry weather in the north favorable for increase. According to Table XXV, something like one year in five has suitable winds. It is doubtful if winds are as favorable as in 1926 even that often. According to figures given in Weather Bureau Bulletin W for several points in western Minnesota, a dry May (with less than 2 inches rainfall) occurs on the average about one year in four. The early wind and later dryness would not be expected to coincide more than one year in twenty, unless they are correlated, which does not appear to be the case. The chance of migrants being abroad in numbers in the southwest, at the time of winds between April 15 and May 15, seems good, but cannot be estimated with our present data.

Summary.

The life history of *Toxoptera graminum* was found to be similar in many respects to that of other common aphids. Life history data are recorded.

Extensive studies under controlled temperatures, both moderate and extreme, have been carried out, for the first time with this species. It has developed from 7° to 33° C., the most rapid development coming at 30°, the maximum reproduction about 22°. It was quickly killed by temperatures as low as −15° or as high as 42°. At temperatures less extreme, but still above or below the range of development killing was slower. Inactivity due to cold was fatal in a few weeks at most. Sexual forms were reared only at temperatures averaging below 22° C. More winged forms appeared at variable temperatures averaging about 15° C. than at other temperatures.

A wide range of relative humidity had little or no direct effect on the species.

When days were shortened to less than 12 hours, at suitable temperatures, sexual forms appeared. They continued to develop as long as days were short. Reproduction rate was much lower with short days; winged forms were more numerous at certain day-lengths.

Rain caused a definite reduction of numbers by mechanical beating off and burial. Snow covering was not fatal; it may give protection against brief cold snaps. Wind was a stimulus and aid to flight.

Food-plants are much injured by feeding because of a characteristic injury, involving destruction of chlorophyll. Many grasses are listed as food plants, but only wheat and oats have been greatly injured. Studies were made of the degree of infestation of some grasses, since little information could be found on this subject. Those studied could be classified as preferred, second-choice and temporary food plants, except some that were not attacked at all. Lessened reproduction and increased migration were encountered on food plants other than preferred. Curtailed or unsatisfactory nutrition tended to stop reproduction and cause migration; it caused a great increase in winged forms in the succeeding generation. Wheat and oats were unsatisfactory as food after the heading stage.

A study of factors producing biological forms was made, for the first time with this species. Winged forms appeared when the parent generation had had poor nutrition, and to a certain extent under variable temperatures averaging about 15° C., as in spring and fall. Some evidence was found of an influence of day-length also. Winged adults produced nearly all wingless progeny under all conditions. Males and oviparous females appeared under a combination of shortened days and temperatures averaging below 22° C.; no other conditions affecting their appearance have yet been noted. Sex-producing influences must be at work two generations before sexes mature; wing-producing influences, more than one generation.

Limited migration on foot, especially by adults and large nymphs, occurred; usually only where food became unsatisfactory. Migration by winged adults took place even when food was satisfactory. Flight depends largely on the wind, and evidence was found of migrations up to several hundred miles in this manner.

Population increase was difficult to calculate because of overlapping generations; developmental rate and reproduction early in adult life are important factors in increase. Potential increase at several temperatures is calculated. It seems likely that a population increase of 13 times per generation may be used as the reproductive capacity of the species. In the field population may reach one to several thousand per square foot before killing grain.

The principal enemies were Coccinellids, Syrphids, and hymenopterous parasites. Chrysopids, Cecidomyids, and general predators are of slight importance. Coccinellids showed great power of control, and held up well in numbers between aphid outbreaks. Syrphids were of less importance. Data on life history and aphid consumption for these two groups are recorded. Hymenopterous enemies have been present only in small numbers, in Minnesota; one species has shown considerable power of control in the south, according to literature.

Toxoptera graminum has been important in lower temperature latitudes where grain is grown, in several continents. In the United States the worst injury has been in the south and border states, especially Oklahoma and Texas.

The species has been most often injurious in regions where rainfall is sufficient for grain-production; but rather light, with long intervals between rains, during the period of injury to grain. In more humid regions injury has often accompanied rainfall shortage. This is ascribed to known reduction of numbers caused by rains.

Summer conditions severely check the green bug, according to the literature and field observations; they include food scarcity, increased migration hazards, and activity of enemies, and in the southern part of the United States, high temperatures.

Wintering in the egg stage is of little economic importance, owing to delay in producing migrants in spring. The sexual forms and eggs seem to develop in the field in Minnesota but seldom, owing to earliness of cold weather. Nymphs and adults winter in the fields in the southern states; winter months having mean temperatures of 30° F. with only few and brief approaches to 0° F. represent about the limit of severity for wintering. A large proportion of the outbreaks occur where this wintering takes place. Migration from wintering places to the north appears to occur in many seasons; usually only part of the distance is covered at one migration, the remainder by later generations. If the infestation becomes established well in advance of summer conditions, considerable injury may result. Usually infestations by migrants is too late to become very important. Conclusions are based on records in the literature, field observations and experiments under controlled conditions.

The 1926 outbreak in the north probably originated from migrants from the southwest. The conditions which existed were such as to make it seem very improbable that other sources were concerned, but were unusually favorable for migration. Winds of dates, direction, and duration suitable to explain infestation occurred; dry weather later was favorable for development. Reports indicate a widespread, though variable, infestation in western Minnesota and Dakota. Migrants leaving the first area in June probably infested territory farther east, where injury seemed to have developed later.

Severe northern outbreaks will probably occur but seldom; that of 1926 seemed to result from a combination of conditions which are not expected to coincide often. Some injury to late sown grain may occur more frequently.

LITERATURE CITED.

Ackerman, Lloyd. 1926. The physiological basis of wing-production in the grain aphid. Jour. Exp. Zool., 44: 1–62.

Ainslie, C. N. 1926. Notes on the recent outbreak of *Toxoptera graminum*. Jour. Ec. Ent., 19: 800–801.

Ashmead, W. H. 1900. Classification of Ichneumon flies or the superfamily Ichneumonoidea. Proc. U. S. Nat. Mus., 23: 1–220.

1903. Classification of the gall wasps and the parasite Cynipoids, or the superfamily Cynipoidea. Psyche, 10: 7–13; 59–73; 140–155; 210–216.

1904. Monograph of the Chalcidoidea. Mem. Carnegie Mus., 4: 225–551. Pls. 9.

Bachmetjew, P. 1901. Experimentelle entomologische studien. I. Temperaturverhalt-nisse bei Inseckten. 160 pp. Leipzig.

Banks, N. A. 1903. A revision of the nearctic Chrysopidae. Trans. Am. Ent. Soc., 29: 137–149. 1 pl.

Bentley, G. M. 1914. Ninth Ann. Rept. Tenn. State Bd. Ent., pp. 120. (Toxoptera treated pp. 27–28.)

Brittain, W. H. 1921. Some factors influencing the occurrence of alate forms in certain Aphididae. Acadian Ent. Soc. Proc., 1921, No. 7.

Chapman, R. N. 1925. Animal ecology with especial reference to insects. Mimeographed. Pp. 370. Minneapolis.

Collins, C. W. 1915. Dispersion of gipsy-moth larvae by the wind. U. S. D. A. Dept. Bul. 273; pp. 21; pls. 6.

Cook, W. C. 1927. Some effects of alternating temperatures on the growth and metabolism of cutworm larvae. Jour. Ec. Ent., 20: 769–782.

Cutright, C. R. 1924. Bionomics of *Hippodamia tridecumpunctata* L. Ann. Ent. Soc. Am., 17: 188–193.

Davidson, J. 1924. Factors which influence the appearance of the sexes in plant-lice. Science, n. s. 59:364.

Davis, J. J. 1916. *Aphidoletes meridionalis*, an important dipterous enemy of aphids. Jour. Agr. Res., 6: 883–887, figs. 4, pl. 1.

Elton, C. S. 1925. The dispersal of insects to Spitsbergen. Trans. Ent. Soc. London, 1925: 289–291.

Ewing, H. E. 1926. Wing-production in plant-lice. Am. Nat., 60: 567–577.

Felt, E. P. 1917. A study of gall midges, VI. 33rd. Rept. N. Y. State Ent., pp. 76–205.

Forbes, S. A. 1905. A monograph of insects injurious to Indian corn. Part II. 23rd Rept. Ill. State Ent., pp. 280, pls. 8, figs. 238.

Gahan, A. B. 1911. Aphidiinae of North America. Md. Agr. Exp. Sta. Bul. 152: 147–200, figs. 11.

Garman, H. 1926. Two important insect enemies of bluegrass pastures. Ky. Agr. Exp. Sta. Bul. 265.

Garner, W. W. and **W. A. Allard.** 1922. Photoperiodism, the response of the plant to relative length of day and night. Science, 55: 582–583.

Girault, A. A. 1917. The North American species of Pachyneuron with three new species (Chalcid flies). Psyche, 24: 88–91.

Glenn, P. A. 1909. The influence of climate upon the green bug and its parasites. Bul. Univ. of Kans., 9: 165–200, figs. 18.

Gregory, Louise H. 1917. The effects of starvation on wing-development of *Microsiphum destructor*. Biological Bul. 33: 296–303.

Hartley, E. A. 1922. Some bionomics of *Aphelinus semiflavus* (Howard). Ohio Jour. Sci., 22: 209–236. 1 pl., 1 fig.

Hayes, W. P. 1922. Observations on insects attacking sorghums. Jour. Ec. Ent., 15: 349–356.

Headlee, T. J. 1914. Some data on the effect of temperature and moisture on the rate of insect metabolism. Jour. Ec. Ent., 7: 413–417.

Headlee, T. J., and **J. W. McColloch.** 1913. The chinch bug. Kans. Agr. Exp. Sta. Bul. 191: 281–353; figs. 13, pls. 6.

Howard, L. O. 1908. Upon the aphis-feeding species of Aphelinus, Ent. News, 19: 365–367.

1921. Rept. of Ent., U. S. D. A., 1921.

Hunter, S. J. 1909. The green bug and its enemies. Bul. Univ. of Kans., 9: 1–163; 201–222; pls. 3, figs. 47.

Kelly, E. G. 1917. The green bug (*Toxoptera graminum* Rond.) outbreak of 1916. Jour. Ec. Ent., 10: 233–248.

Lefroy, H. 1908. Imported insect pests. Agr. Jour. India, 3, part 3: 237–244.

Luginbill, P. 1914. South Carolina Dept. Agr. Rept. 10, p. 264. (In S. C. Yearbook for 1913.)

Luginbill, P., and **A. H. Beyer.** 1918. Contribution to the knowledge of *Toxoptera graminum* in the south. Jour. Agr. Res., 14: 97–119, pl. 1, figs. 8.

Marcovitch, S. 1924. The migration of the Aphididae and the appearance of the sexual forms as affected by the relative length of daily light exposure. Jour. Agr. Res., 27: 513–522.

McAtee, W. L. 1913. Relations of birds to grain aphids. U. S. D. A. Year Book, 1912, pp. 398–404.

Merriam, C. H. 1895. The geographical distribution of animals and plants in North America. U. S. Dept. Agr. Year Book, 1894: 203–214.

Metcalf, C. L. 1911–1913. Life history of Syrphidae. Ohio Naturalist (now Ohio Jour. Sci.). Parts in Volumes 11, 12, 13.

1916. Syrphidae of Maine. Maine Bul. 253, pp. 72, pls. 9.

Moore, W. 1914. A comparison of natural control of *Toxoptera graminum* in South Africa and the United States. Ann. Ent. Soc. Am., 7: 77–85. (A fuller treatment is given in Agr. Journ., Union of S. Africa, Vols. 6 and 7, 1913–14.)

Morrill, A. W. 1913. Notes on important insects of the year. Fifth Ann. Rept. Ariz. Comm. Agr. and Hort., pp. 33–48.

Palmer, M. A. 1914. Some notes on life history of lady beetles. Ann. Ent. Soc. Am., 7: 213–238. 3 pls.

1917. Additional notes on heredity and life history in the Coccinellid genus *Adalia* Mulsant. (Contains records of hibernation of *Hippodamia convergens*.) Ann. Ent. Soc. Am., 10: 289–302.

Phillips, W. J. 1915. Further Studies on the Embryology of *Toxoptera graminum*. Jour. Ag. Res., 4: 403-404, 2 plus.

Piper, C. V. 1924. Forage plants and their culture. Pp. 671. Macmillan Co.

Reinhard, H. J. 1927. The influence of parentage, nutrition, temperature and crowding on wing-production in *Aphis gossypii* Glover. Texas Agr. Exp. Sta. Bul. 353: 19.

Rondani, C. 1852. Lettera al L. Prof. G. Bertoloni: Nota sopra una specie di Afide, volante in numerosa torma nella citta' di Parma. Nuova Ann. Sci. Nat. Bologna, Ser. III, T. 6, pp. 9–12.

Ruggles, A. G., and **F. M. Wadley.** 1927. The green bug in Minnesota. Jour. Ec. Ent., 20: 321–327. 1 fig.
Sanborn, C. E. 1916. The green bug. Okla. Agr. and Mech. College, Ext. Circ., 30: 4.
Sanborn, C. E., W. J. Brown and **G. A. Bieberdorff.** 1926. Entomology. In Bien. Rept. Okla. Exp. Sta., 1924–26, pp. 38–43.
Sanderson, E. D. 1908. The relation of temperature to the hibernation of insects. Jour. Ec. Ent., 1: 56–65.
Shinji, G. O. 1918. A contribution to the physiology of wing-development in aphides. Biol. Bul. 35: 95–116.
Shull, A. F. 1926, 1927. Papers on duration of light and life cycle of aphids. Abstracts in Anat. Rec., 34: 168; 37: 136.
Smith, R. C. 1922. The biology of the Chrysopidae. Cornell Mem. 58: 72, pls. 14, figs. 10.
Stevens, N. M. 1905. A study of the germ cells of *Aphis rosæ* and *Aphis aenotheræ*. Jour. Exp. Zool., 2: 213–334.
Tucker, E. S. 1918. Notes on the green bug (*Toxoptera graminum* Rond.) in Texas. Trans. Kans. Academy of Sci., 28: 276–291.
Van der Goot, P. 1915. Beitrage zur Kenntniss der Hollandischen Blattlause. Pp. 600. Berlin.
Viereck, H. L. 1916. The Hymenoptera, or wasp-like insects, of Connecticut. Conn. Geol. and Nat. Hist. Survey, Bul. 22: 824, pls. 10, figs. 15.
Wadley, F. M. 1923. Factors affecting the proportion of alate and apterous forms of aphids. Ann. Ent. Soc. Am., 16:279–303, figs. 2.
1929. Observations on the injury caused by *Toxoptera graminum* Rond. (Homoptera: Aphididæ). Proc. Ent. Soc. Wash., 31: 130–134.
Walton, W. R. 1921. The green bug or spring grain aphis. U. S. Dept. Agr. Farmers' Bul. 1217. Pp. 11, figs. 9.
Washburn, F. L. 1908. A. The so-called "green bug" and other grain aphids of Minnesota in 1907. Univ. of Minn. Agr. Exp. Sta. Bul. 108, pp. 257–280, pl. 1, figs. 15. (First published as a special report.)
1908. B. The spring grain aphis or the so-called "green bug." In 12th Rept. State Ent. of Minn., pp. 42–46.
1908. C. Sexual forms of *Toxoptera graminum* Rond. Can. Ent., 40: 53–54.
Webster, F. M. 1892. Notes on the grain Toxoptera. Insect Life, 4: 245–248.
1914. An unrecorded parasite of *Toxoptera graminum*. Jour. Ec. Ent., 7: 403–404.
1916. The spring grain aphis or "green bug" in the southwest, and the possibilities of an outbreak in 1916. U. S. D. A. Office of Secr., Circ. 55. Pp. 3, figs. 3.
Webster, F. M., and **W. J. Phillips.** 1912. The spring grain aphis or green bug. U. S. Bu. Ent., Bul. 110, n. s., pp. 144, pls. 9, figs. 48, diagrams 5.
Wilson, E. B. 1925. The cell in development and inheritance. Pp. 1232, figs. 529. Macmillan Co.

THE HABITS OF LEAF-MINING COLEOPTERA ON BARRO COLORADO ISLAND, PANAMA.

S. W. Frost,
The Pennsylvania State College.

The writer spent several months on Barro Colorado Island, Canal Zone, Panama, rearing and studying leaf-mining insects. The Coleoptera of the familes Chrysomelidæ, Curculionidæ and Buprestidæ have been studied sufficiently to warrant a few notes concerning their habits. The drawings were made, and notes taken, while on the Island. The host plants were determined by Dr. Paul C. Standley of the Field Museum of Natural History, Chicago, Ill. The Buprestidæ were determined by Mr. W. S. Fisher and the Curculionid identified by Mr. L. L. Buchannan both of the U. S. National Museum. One species from Panama City is added.

The Chrysomelidæ (Hispini) were the most numerous of the leaf-mining Coleoptera. The mines of these species were scattered, seldom more than one or two on a single plant, and it was necessary to do considerable collecting in order to get sufficient material to rear and study their habits. The adults were frequently collected as they were found resting or feeding on their food plants. All of the Chrysomelidæ have been turned over to the National Museum for identification and study. At present the group is not in satisfactory condition and it will require some time before the material can be properly worked up.

The remaining leaf-mining Coleoptera consist of a single Curculionid, *Prionomerus abdominalis* Boh., and a few Buprestidæ. The mines of some of the Buprestidæ were abundant while others were scattered, a single plant bearing but one or two mines. The adults of a few species were collected while feeding or ovipositing on their favorite food plants.

Prionomerus abdominalis Boh., (Plate I, Fig. 2) probably represents one of the extremes in leaf-mining insects. While we usually think of a miner as an insect producing a more or less flat mine within the leaf, this species produces a large mussy blotch that bulges three quarters of an inch when the larvæ have completed their growth and spun their

cocoons within the leaf. They mine the leaves of Lauraceae, making large blister-like mines that cover over one half or three quarters of the leaf surface. The eggs, six or seven in number, are inserted in the lower side of the leaf usually near a vein at the base of the leaf. At first the larvæ produce a broad linear mine which follows the edge of the leaf and is crowded with an abundance of black frass. Later the larvæ work towards the center of the leaf and mine an area somewhat devoid of frass. All of the larvæ continue to mine and complete their growth in the same leaf. When ready to transform, a large ball, one half or three quarters of an inch in diameter, is formed in the center of the mine composed apparently of a malpighian secretion. This has the appearance of coarse black silk. Within this mass the larvæ make individual cells. The adults emerge in the mine and cut their way to freedom through the surface of the leaf.

Hylaeogena alibertiæ Fisher, (Plate I, Fig. 1). This species was described in Ent. Soc. Wash 31, 1929 from a specimen reared by the writer from the host plant *Alibertia edulis* (L. Rich) A. Rich. The leaves of this plant are small and a single larva mines a leaf. The mine starts at the base of the leaf where the egg is laid. The first part of the mine is jammed with abundant frass but as the mine is broadened the frass is arranged in a more or less neat central band. Nearly the whole leaf area is mined before the larva matures. A circular case is cut from the two leaf surfaces and within this the larva spins a transparent silken cocoon.

Hylaeogena coelicolor Obenb., (Plate I, Figs. 3 and 4), was reared on several occasions from a plant which has not been determined. A batch of three or four eggs are laid on the underside of the leaf and covered with a mass of excrement or regurgitated food. This material is yellow in color and laid down in streaks as though applied with the mouth. On hatching the larva makes a short, linear mine, then produces a blotch covering about three quarters of the leaf surface. The mine is green in color and visible from both surfaces of the leaf, but more plant tissue is removed from the upper than the lower side of the leaf. The frass is laid down in zig zag bands. The larva cuts a circular case from the leaf, the upper and lower epidermal layers forming the upper and lower sides of the case respectively. To emerge the adult cuts a circular cap considerably smaller than the diameter of the case.

Pachyschelus atroviridis Fisher, (Plate II., Figs. 7 and 8), is one of the most abundant species of leaf-mining Buprestidæ on Barro Colorado Island. The food plant, Serjania, is likewise common and forms one of the conspicuous low growing plants. The adults were often seen feeding or ovipositing in considerable numbers on this plant. Sometimes as many as twenty-five or thirty adults were seen on a single plant and almost every leaf showed eggs or mines. Two or three eggs are laid on the under side of the leaf between two of the larger veins and covered with a triangular patch of excrement or regurgitated food. This covering is securely fastened at the base but loose at the

distal end. It consists of two thin layers of material rather than a thick mass. When the eggs hatch the larvæ enter directly into the leaf and make at first a short linear mine. Later the mine is broadened considerably. The frass is scattered in irregular masses and in the narrower portions is laid down in short arc-like bands. When ready to transform, the larva cuts a circular case from the leaf. This operation was observed many times. The larva clears a circular area in the mine of the desired size (the same diameter as the length of the larva). This area is transparent with only the larger veins left, giving it a skeletonized appearance. A cleaner job is done than in the rest of its operations where more cells are left on the floor of the mine. The larva then commences cutting the two surfaces of the leaf about the edge of the circular area stopping now and then to spin a few threads to hold the upper and lower portions of the case together. In about two hours the case is entirely severed from the leaf with the exception of three or four larger veins which hold the case in position until the larva is ready to abandon the leaf. When sufficient silk has been spun to properly fasten the upper and lower portions of the case together, the larva severs these ties by violent movements of its head. The drying of the veins also assist the larva in freeing itself from the leaf. Finally the little case pops from the leaf with considerable force. Those observed at the laboratory were sometimes carried for several inches. The following day the larva is much shrunken and enveloped in considerable silk but the pupa is not formed until the second day after the larva starts the construction of its case. The completed case is opaque and brown in color.

Pachyschelus atrifrons Fisher, (Plate II, Figs. 5 and 6) was fairly common but the writer seldom found more than one or two mines on a single plant. The larvæ mine the leaves of *Acalypha diversifolia* Jacq. The mine starts as a narrow trail along the edge of the leaf, gradually becoming broader until a distinct blotch is produced. At first the frass is laid down in a central line but later it is scattered in an irregular band along the sides of the mine. Transformation occurs in a semitransparent, papery cocoon spun in the mine.

Pachyschelus psychotriae Fisher (Plate III, Figs. 12, 13, 14). Three eggs were laid on the underside of a leaf of *Psychotria carthaginensis* Jacq. These eggs were covered with a gelatinous scale like mass probably from the mouth of the beetle. One of the eggs hatched and produced a long mine, at first quite narrow and crowded with frass but later becoming broad with the frass scattered along the sides of the mine. The larva spins a silken cocoon within the mine that is securely fastened to the bottom of the mine and is covered with yellow frass pellets.

Pachyschelus frosti Fisher. A single female was collected on Burro Colorado Island, but its food plant and nothing concerning its habits are known.

Brachys fulgidus Fisher (Plate IV, Fig. 15). The mines of this species were collected by Mr. August Busck in Panama City on the

leaves of *Ficus elastica* Roxb. The original description and habits of the miner appear in Proc. U. S. National Museum, Vol. 62, Art. 8, pages 44-45, 1922. The mines are conspicuous and sometimes as many as twelve were found on a single leaf.

A mine of Brachys was found on *Faramea occidentalis* (Plate IV, Fig. 16). A single egg is laid on the upper side of the leaf. The mine is at first narrow with a moderate amount of frass, later it broadens into a more or less blotch mine with the frass arranged along the edges of the mine. The naked pupa was found in the mine but the adult was not reared.

Another species of Brachys was frequently seen on Inga spp. (Plate IV, Fig. 17) but the adults were never reared. Apparently the larva escapes from the mine to pupate, for all of the mines show distinct round holes through the lower side and no pupæ were found in the mines.

On *Phryganocydia corymbosa* (Plate III, Fig. 10-11) a very characteristic mine was often collected but unfortunately adults were not reared. There are two parts to the mine, one filled with abundant black frass and the other almost without frass. The larva spins a pupal case of silk in the mine which is suspended between the two surfaces of the leaf by small masses of frass. Larvæ were examined by Dr. Adam Böving and he states that they belong to the group Pachyschelus.

It is evident that our knowledge of the leaf-mining Coleoptera of the American tropics is scant. Many adults of leaf-mining insects have, of course, been taken but the collector has too often shown no primary interest in their habits or food plants. Aside from the Buprestidæ, practically no studies have been made of the life-histories of tropical leaf-mining Coleoptera. Even the habits of certain genera of this group namely: Lius, Liopleura, Liopleurella and Callimiora, are little known. It is believed that they are largely leaf–mining species. Tropical Hispini are numerous, little studied and difficult to identify. The writer's material, which comprise the most extensive group reared and studied in the tropics, awaits determination. The Curculionid leaf-miners are probably somewhat limited in numbers and at present are known only from the genus Prionomerus. Orchestes, a large genus having its origin and greatest development in Europe, and at present unknown in the tropics, may yield some interesting species.

European students of leaf-mining insects have not collected in the tropics. As in America, systematists have collected extensively. The field for the study of leaf-mining insects in the Old world tropics is open.

The abundant systematic writings of Schwartz, Blatchley, Leng, Horn, Van Duzee, Chevrolet, Champion, Hamilton and others have included many notes on tropical species of Florida and the West Indies. Van Dyke and Fall have contributed to tropical species of California. The Biologia Centrali Americana lists a great many tropical species and numerous food plants. The only outstanding papers on tropical leaf-mining Coleoptera are those by Mr. W. S. Fisher on the Buprestidæ.

BIBLIOGRAPHY.

Fisher, W. S. The Leaf-mining Buprestid Beetles of Mexico and Central America. Proc. U. S. Nat. Mus. 62, art. 8: 1–95, 1922.

A Revision of the West Indian Coleoptera of the Family Buprestidae. Proc. U. S. Nat. Mus. 65, art. 9: 1–207, 1925.

New Species of Buprestid Beetles from Costa Rica. Proc. U. S. Nat. Mus. 76, art. 6: 1–10, 1929.

Notes on Leaf-mining Buprestidae (Coleoptera) with Descriptions of New Species. Proc. Ent. Soc. Wash. 31, No. 9: 177–182, 1929.

A New Leaf-mining Buprestid from the Canal Zone (Coleoptera). Proc. Ent. Soc. Wash. 33, No. 2: 42–43, 1931.

EXPLANATION OF PLATES.

PLATE I.

(Slightly reduced.)

Fig. 1. Mine of *Hylaeogena alibertiæ* Fisher on *Alibertia edulis*.
Fig. 2. Mine of *Prionomerus abdominalis* Boh., on Lauraceæ.
Fig. 3. Mine of *Hylaeogena coelicolor* Obenb., plant undetermined.
Fig. 4. Pupal case of *Hylaeogena coelicolor* Obenb.

PLATE II.

(Slightly reduced.)

Fig. 5. Pupal case of *Pachyschelus atrifrons* Fisher.
Fig. 6. Mine of *Pachyschelus atrifrons* Fisher on *Acalypha diversifolia*.
Fig. 7. Gelatinous covering over eggs of *Pachyschelus atroviridis* Fisher.
Fig. 8. Mine of *Pachyschelus atroviridis* Fisher on Serjania sp.
Fig. 9. Undetermined Coleopterous miner.

PLATE III.

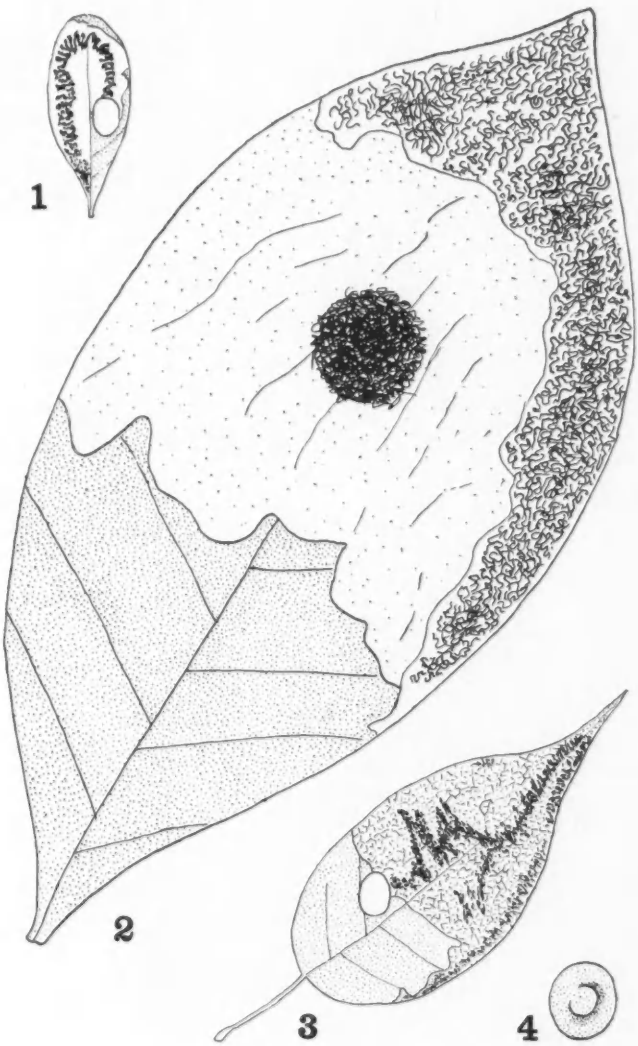
(Slightly reduced.)

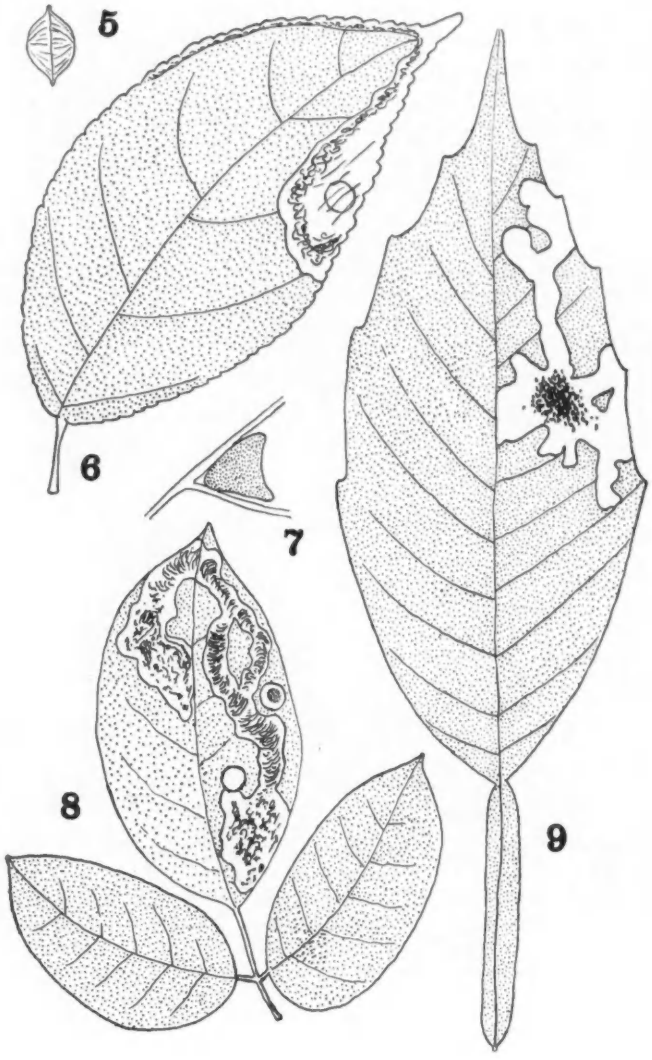
Fig. 10. Pupal case of undetermined species of *Pachyschelus* on *Phryganocydia corymbosa*.
Fig. 11. Mine of the above species on *Phryganocydia corymbosa*.
Fig. 12. Side view of pupal case of *Pachyschelus psychotriae*.
Fig. 13. Mine of *Pachyschelus psychotriae* on *Psychotria carthaginensis*.
Fig. 14. Top view of pupal case of *Pachyschelus psychotriae*.

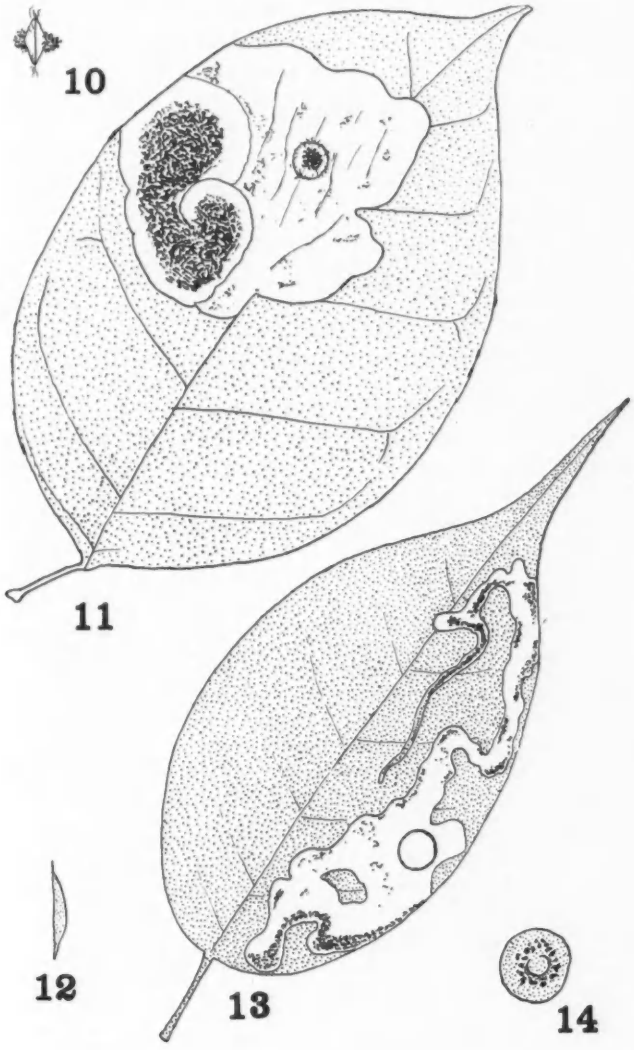
PLATE IV.

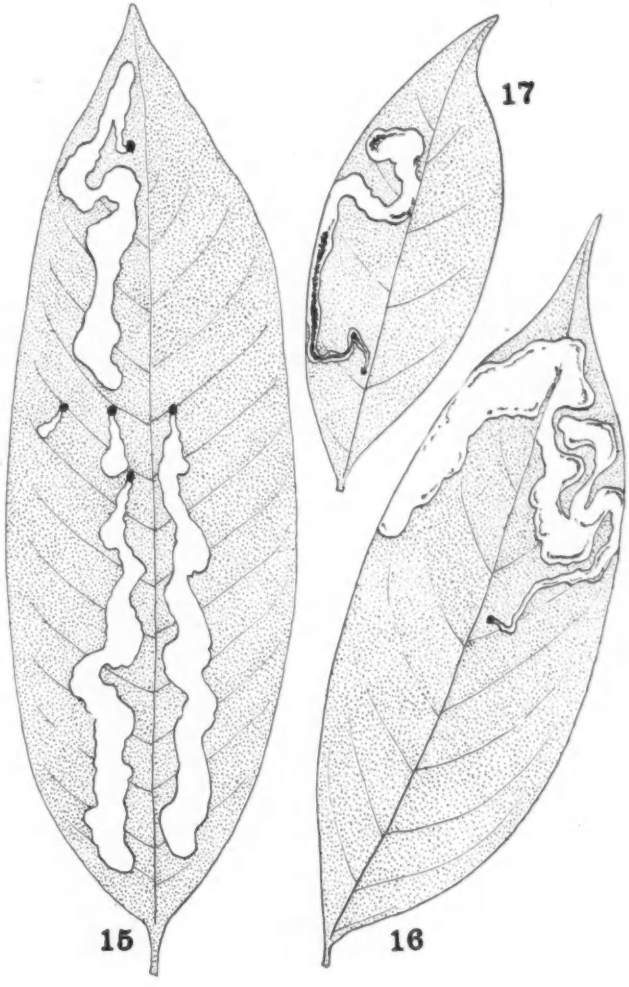
(Slightly reduced.)

Fig. 15. Mine of *Brachys fulgidus* Fisher on *Ficus elastica*.
Fig. 16. Mine of *Brachys* sp. on *Faramea occidentalis*.
Fig. 17. Mine of *Brachys* sp. on *Inga* sp.


1
2
3
4


5
6
7
8
9


10
11
12
13
14


17
15
16

A ONE-EYED BEE (APIS MELLIFICA).*

ERWIN C. ALFONSUS,
Division of Entomology and Economic Zoology,
University of Minnesota,
St. Paul, Minnesota.

During an experiment on labor division in a bee colony, a daily marking of newly emerged bees with color-dots on the thorax or abdomen was undertaken. August 4, 1930, a colony of Italian bees was opened for the purpose of marking the young bees. On the inner surface of the inner cover, a few bees were crawling around. Three or four of these were without marking and hence were bees that had emerged within the previous twenty-four hours, the time when the last marking of bees took place. One of these bees attracted my attention by its unusual manner of locomotion. It moved slowly as all young bees do, but backwards instead of forward, in a manner characteristic of crayfish. Taking the specimen in my hand I noticed its extremely narrow face. An examination under the binocular microscope revealed the fact that I was dealing with a freak bee, a bee with only one compound eye. This was situated in the middle of the head, in the frontal region, symmetrically placed. In the laboratory the specimen continued to march backwards and ate in a normal manner the droplets of honey which I offered it from the tip of a toothpick. I could not make it crawl forward even though I placed the honey a short distance in front of its head.

The pictures show the one-eyed specimen with one of its normal sisters of the same age (Plate I, Figs. 1 and 2).

A closer examination showed that the abdomen, with the sting, was normally developed. The thorax and its appendages also could not be differentiated from those of its normal sister. Pollen collecting apparatus was fully developed, the wing venation appeared normal.

As far as the head region is concerned several changes were noticed. The ocelli were absent. The single compound eye was crescent-shaped, with two pointed ends instead of

*Published as Paper No. 1008 of the Journal Series of the Minnesota Agricultural Experiment Station.

kidney-shaped, as in the normal worker. One compound eye of the normal worker, as shown in the illustrations, consists of approximately 5082 ommatidia. In the one-eyed specimen the ommatidia are much larger, because the one eye has the same area as the normal compound eye, but consists only of approximately 3525 ommatidia.

The vertex is swollen and, in combination with the occiput and the genæ, it represented a ring-like structure, interrupted only by the insertion of the mouthparts. The mouthparts were normally developed and showed exactly the same dimensions as the mouthparts of the normal sister. The antennæ of the one-eyed specimen were shorter and thicker and, even though the face was narrower, the bases of the antennæ were further apart than normal. Between the bases there is a tuft of fine, branched hairs.

To give a clearer picture of the dimensions of the various parts of the head, a few careful measurements were taken on the abnormal specimen and, for the sake of comparison, on the normal sister. These data are as follows:

Measurement	One-eyed Bee, mm.	Normal Bee, mm.
Diameter of antennal scape	0.395	0.225
Length of antennal scape	1.35	1.6
Distance between the antennal bases	0.6	0.27
Diameter of flagellum	0.315	0.225
Length of flagellum	2.925	3.375
Width of labrum	1.215	1.325
Length of labrum	0.3375	0.2925
Width of clypeus	1.6425	1.171
Length of clypeus	1.3050	1.2575
Width of compound eye	1.035	1.0575
Length of compound eye	2.6	2.565
Width of head	3.2175	4.1625
Length of head	3.87	3.7125

Repeated thorough examinations of the colony, from which the abnormal specimen was obtained, failed to reveal any bees with similar characteristics. The above described species has been placed for reference in the entomological collection of the University of Minnesota, St. Paul, Minnesota.

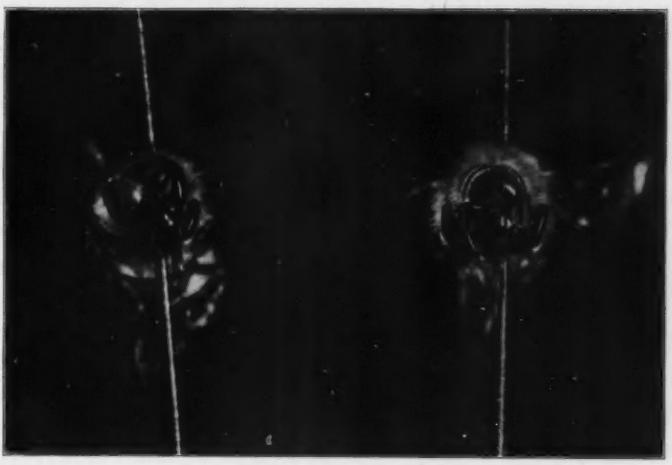


Fig. 1. Honey Bee—Front View.
Left, showing normal bee. Right, specimen with single eye.

Fig. 2. Honey Bee—Side View.
Left, showing normal bee. Right, specimen with single eye.

THE BIOLOGY OF TABANUS LINEOLA FABR.*

H. H. SCHWARDT,
Department of Entomology,
University of Arkansas.

Most studies of North American Tabanidæ have been concerned largely with taxonomy and distribution, with the result that no complete biological study of any species has been made. Hine (1), who was the first investigator to rear a tabanid species from egg to adult, obtained an adult of *Tabanus lasiophthalmus* from the larvæ hatching from one egg mass. Webb and Wells (10) succeeded in rearing three individuals of *T. punctifer* from egg to adult in an average time of 671 days, or about a year and ten months. Stone (9) obtained one adult from an egg mass of *T. atratus*, the black horse-fly. The developmental period was 357 days. Mitzmain (6), working in the Philippine Islands; Neave (7), in Nyasaland; and Isaac (3), in India, have recorded important facts in the life histories of several exotic species. The contributions of workers who have collected Tabanidæ as larvæ and reared them to the adult stage, thus securing partial, but nevertheless valuable records on life histories, have been summarized in a recent paper (8).

This paper is based on life history records of 202 individuals of *T. lineola*, which have been reared from egg to adult under conditions permitting daily observation of all the stages. Field studies on all the stages have accompanied the insectary work. The average incubation period was found to be 4 days, the average larval period 48.8 days, the average pupal period 8.1 days, and the preoviposition period 9 days. The total developmental period has an average duration of 69.9 days. At least two generations occur in Washington County, Arkansas, where all the data recorded here were obtained.

Tabanus lineola is a widely distributed species of horse-fly. Hine (2) records it as "common in eastern North America, and known from as far west as Arizona." He found it to be one of the worst of stock pests in Louisiana. The species is common in most of Arkansas and is exceeded in numbers only

*Research Paper No. 219, Journal Series, University of Arkansas.

by *T. costalis*. The adult fly is characterized chiefly by its brilliant green eyes, which are crossed by more than one transverse purple eye stripe (usually two and a partial third), and by the brown or black abdomen which bears three longitudinal, dorsal grey stripes. The length of the fly varies from 12-15 mm.

METHODS.

The rearing technique which proved successful for *T. lineola*, and which subsequently has proved favorable for several other species of Tabanidæ, is not greatly different from that used by Hine (1) for *T. lasiophthalmus*. Half-pint jelly glasses with perforated tin lids were used for cages. These contained half an inch of fine sand which was kept nearly saturated with water. The cages were set with one edge elevated so that their floors formed a fifteen-degree angle with the table, and thus established in each cage a moisture gradient varying from moist sand to sand completely saturated with water. Earthworms, snails, and Crustacea were found to be favorable foods, but the latter were finally used exclusively because they were most easily obtained. The meat from the abdomen of one large crayfish will feed twenty-five nearly grown larvæ for twenty-four hours.

Egg masses were kept in jelly-glass cages until hatching occurred. Immediately after hatching the larvæ from each egg mass were counted. Each larva to be reared was then removed on a wet camel's hair brush and placed in a separate cage, care being exercised to see that each was placed on a particle of food. The larvæ were fed, and all old food removed once every twenty-four hours thereafter until transformation occurred. To locate the small larvæ for observation, and to find their cast skins, the cages were flooded to a depth of about one inch and the contents stirred gently with a brush. When the sand settled the larvæ and any exuvia which they had cast floated at the surface. It was impossible to find the first few exuvia without flooding the cages, and flooding aided greatly in locating even the last skin. It also helped to keep the cages clean. No special care was required at the time of transformation. The pupæ were almost invariably found lying on the surface of the sand.

THE EGG.

Eggs of *T. lineola* are always deposited in masses, which if complete are approximately 10 mm. long by 4 mm. wide, and rounded or pointed at both ends. The individual egg is spindle-shaped, smooth, and about 1.6 mm. long by .3 mm. in thickness. The eggs at the sides of the mass slope downward, forming an angle of about 45 degrees with the median, while those at the center of the mass parallel the median. Incomplete masses, which are the rule, are less than 10 mm. long and are square instead of rounded or pointed at the lower edge. Freshly deposited eggs are milky white in color, but within six hours they become light grey. After twenty-four hours they are dark lead grey, which color they retain until hatching occurs. Occasional masses become almost black before hatching.

Seven egg masses collected in the field produced 454, 155, 267, 363, 364, 376, and 243 larvæ respectively, or an average of 317 larvæ.

THE INCUBATION PERIOD.

The incubation period as observed under insectary conditions varied from 3 to 5 days. Five masses upon which definite observations were made required 5, 4, 3, 4, and 4 days respectively, or an average of 4 days. Temperature is probably the most important factor influencing the incubation period, and eggs exposed to direct sunlight in the field probably hatch more rapidly than those kept in the insectary.

TABLE I.

Tabanus lineola Fabr. Larval Period. Fayetteville, Arkansas, 1930.

Length of Larval Period, (Days)	Number of Larvae	Length of Larval Period, (Days)	Number of Larvae	Length of Larval Period, (Days)	Number of Larvae
29	2	46	6	64	1
30	3	47	8	65	1
31	2	48	3	66	2
32	5	49	6	68	1
33	10	50	6	69	3
34	5	51	5	70	3
35	9	52	4	71	5
36	4	53	1	72	3
37	5	54	3	73	1
38	7	55	2	74	1
39	11	56	8	78	1
40	7	57	14	79	1
41	4	58	4	82	1
42	4	59	4	83	1
43	11	60	1	86	1
44	4	62	1	87	2
45	2	63	1	90	1
				92	1

Average larval period.....48.8 days

THE LARVA.

The full grown larva of *T. lineola* when in a resting position is approximately 21 mm. long and 3.2 mm. wide. The color is usually white, but some larvæ take on a slightly yellow or pink cast just before pupation. In common with other larvæ of the genus Tabanus, the larva of this species is spindle-shaped, tapering almost to a point at both ends. The head is small, cylindrical, tapers slightly anteriorly, and can be entirely retracted into the thorax. For a detailed description of a larva of this genus see Webb and Wells (10).

THE LARVAL PERIOD.

The larval period of *T. lineola* is comparatively short. Twenty-two individuals reared during the summer of 1930 required 33 days or less to complete their respective larval periods, and the average for 202 individuals was only 48.8 days (Table I). The longest and shortest

larval periods observed were 92 and 29 days, respectively. It seems probable that all eggs which hatch before about August 1 produce adult flies before the winter immediately following. Of a series of larvæ which hatched on July 25, 1930, every individual which survived had produced an adult by September 27, 1930.

In the field, larvæ are usually found in the mud bordering lowland ponds or sluggish water courses.

During the spring of 1930, larvæ were collected from February 12 until May 20. Of the 14 larvæ which completed the cycle, 12 had emerged as adults by June 21, one required until June 30, and the last adult emerged July 11.

NUMBER AND DURATION OF LARVAL STAGES.

The larvæ of *T. lineola* normally pass through four or five larval stages. Variations were observed in which three to seven larval

TABLE II.

Tabanus lineola Fabr. Duration of Larval Stages in Days. Fayetteville, Arkansas, 1930.

Instar	Maximum	Minimum	Average	Number of Larvae Observed
First	31	5	12.3	195
Second	14	2	4.6	195
Third	61	1	7.8	195
Fourth	63	1	16.6	168
Fifth	67	3	21.9	66
Sixth	47	5	23.7	12
Seventh	18	18	18.0	1

stages occured, but these were comparatively rare, and it seems probable that some larvæ may have consumed their cast skins occasionally, thus reducing the apparent number of larval stages. The prepupal period was poorly defined in all larvæ observed and is treated as a part of the last larval stage in data presented on stages. Just before transforming, the larvæ undergo a resting period, the beginning of which is indicated by the invagination of the head, and the refusal of food. This period of resting varies in duration from 1 to 57 days. Of 195 larvæ on which observations were made, 27 had 3 larval stages, 100 had 4, 56 had 5, 11 had 6, and 1 larva had 7 stages. An enormous variation occurs in the duration of each of the larval instars, as shown in Table II.

The larvæ of several species of Tabanidæ molt almost immediately after hatching. This has been observed for *T. punctifer* and *T. phaenops* by Webb and Wells (10), for *T. atratus* by Stone (9), for *Chrysops callidus* by Marchand (5), and for several Indian species by Isaac (3). Larvæ of *T. lineola* have never been observed to molt sooner than five days after hatching.

THE PUPA.

The pupa of *T. lineola* is 14 mm. long, and 3 mm. wide at the thoracic region. The color is white just after transformation, but within two hours it has changed to light brown, which color it retains until the adult emerges. A double row of large spines encircles the posterior border of abdominal segments 2-7. A pair of large, raised, lateral spiracles are present on each abdominal segment from 1 to 7 inclusive. The abdomen is terminated by six large spines which in this species lie in two straight rows, with four spines in the dorsal row and two in the ventral row. For a detailed description of a pupa of this genus see Stone (9).

THE PUPAL PERIOD.

The pupal period of *T. lineola* is of short duration. For 201 pupæ on which observations were made, the period varied from 5 to 16 days, the majority requiring from 7 to 9 days. (Table III.)

TABLE III.

Tabanus lineola Fabr. Duration of the Pupal Period.
Fayetteville, Arkansas, 1930.

Pupal Period, (Days)	Number of Pupae	Pupal Period, (Days)	Number of Pupae
5	2	11	11
6	28	12	3
7	61	13	2
8	35	14	1
9	29	16	1
10	28		

Average pupal period.....8.1 days

The duration of the pupal period appears to be influenced by temperature, higher temperatures hastening development. The uniformly high temperatures which prevailed during the summer of 1930 made observations on this point of small value.

Pupæ of this species do not require a drier environment than larvæ. In many instances pupæ half submerged in water have developed, and the adults have emerged without difficulty. The greater danger in fact, appears to be that of keeping them too dry. Practically all transformations occurred on the surface of the sand. The adults emerged with ease even though the pupal cases were not partly embedded in the sand, as appears to be true in the natural environment.

Pupæ are difficult to find in the field. A single pupa taken August 22, 1930, in the mud border of a small pond, produced an adult August 28.

THE ADULT.

The adults of *T. lineola* have been taken in the field from May 4 until October 9. They are present in large numbers throughout the season, except for the brief period between generations which occurs in the latter part of July.

During the summer months they begin flying and feeding at about 9:00 A. M. and continue their activities until 6:00 P. M. They appear to prefer cattle as hosts, even when horses or mules are near by. They will occasionally attack a man. When obtaining a meal of blood, several punctures are made, and the pain and annoyance to the host thereby multiplied.

Males are seldom seen in the field. They have been taken occasionally at water, or on flowers.

THE PREOVIPOSITION PERIOD.

A preoviposition period of 9 days was recorded for the only reared fly which fed and oviposited in captivity. This female emerged August 5, at which time it was put in a cage with a male. Both male and female fed greedily on dilute honey provided as food. The female refused to feed on an animal until August 11, when it fed till the abdomen was completely distended. By the following morning the abdomen had resumed its normal proportions. On August 14, which was 9 days after emergence and 3 days after the meal of blood, a normal-sized egg mass was deposited. The mass did not hatch, and remained white, instead of becoming dark grey as all field-collected eggs of this species do. This female refused to feed again after oviposition and died August 29. Mating of this species has never been observed, either in cages or in the field. A second female, treated like the first, emerged July 30, fed on a cow August 11, but deposited no eggs. It died August 25.

OVIPOSITION.

In the insectary oviposition was readily obtained in cages on either rice or barnyard grass. Cylindrical screen wire cages sixteen inches long and eight inches in diameter were used. One end was covered with muslin, and the other rested on the soil in a stone jar. Rice or barnyard grass about twelve inches tall was set in the soil so that it projected up into the cylinder. The soil was kept covered with water to a depth of an inch. Female flies taken in the field during, or soon after feeding were placed in the cages and oviposition usually occurred within a week. No male flies were kept in the cages. Oviposition occurred more frequently when the cages were kept in direct sunlight. A piece of cotton saturated with dilute honey was kept in each cage, and occasionally a fly was seen feeding on the liquid.

Approximately half an hour is required to deposit a complete egg mass containing from 350 to 400 eggs. During the process of oviposition the fly stands head downward and moves forward as successive layers of eggs are placed.

NUMBER OF GENERATIONS.

Eggs have been taken in the field from June 2 until August 14, and they probably occur much later. They have usually been found on low-growing vegetation at the water's edge. No particular plant seems to be preferred as a place for oviposition, and if plants are absent, pieces of wood appear to be quite as acceptable. In the rice-growing section of Arkansas, egg masses of *T. lineola* have frequently been seen on young rice which has just been flooded.

TOTAL DEVELOPMENTAL PERIOD.

The total developmental period as obtained from averages of the egg, larval, pupal, and preoviposition periods is 69.9 days.

It has been generally conceded in the literature that all species of North American Tabanidæ have but one generation a year, and that some require more than a year for complete development. Hine (1) believes that *T. stygius* probably hibernates twice before entering the adult stage. The *T. lasiophthalmus* reared by Hine (1), *T. punctifer* reared by Webb and Wells (10), and *T. atratus* reared by Stone (9), all required one winter of hibernation before the adult emerged.

Tabanus lineola has at least two generations a year in Arkansas. Of the larvæ issuing from four egg masses hatching June 6, 1930, June 23, 1930, July 3, 1930, and July 25, 1930, respectively, all of the 202 larvæ which survived had pupated by September 20, 1930, and the adults had all emerged by September 27. Eggs obtained from one of these flies in a cage were infertile. In the field a second generation would be necessary to carry the species over winter.

Field observations of adult flies and egg masses show that two generations probably occur in Arkansas. A rapid decline in the number of adults and egg masses found in the field occurs during mid-July, after which their numbers again rise and remain fairly constant during the remainder of the season. Adults were first taken May 4, and they increased in abundance until June 21, when they had assumed outbreak proportions in certain localities. During early July their numbers fell until July 18 and 19, on which days not a single fly could be found, and no egg masses were found in the usual places. One fly was taken on July 22, and two were found the following day. From

then on their numbers increased slowly, and egg masses were again found in the places where they had occurred in the spring.

LITERATURE CITED.

1. **Hine, J. S.** 1906. Habits and life histories of Tabanidae. U. S. D. A. Bur. Ent. Tech. Ser. Bul. 12, pp. 19–38.
2. **Hine, J. S.** 1907. Second report upon the horse-flies of Louisiana. La. Agr. Expt. Sta. Bul. 93.
3. **Isaac, P. V.** 1924. Papers on Indian Tabanidae. I, II, III. Mem. Dept. Agr. India, Ent. Ser. VIII, No. 5, pp. 53–62.
4. **King, H. H.** 1914. Notes on the bionomics of *Tabanus taeniola*, and *Tabanus ditaeniatus*. Bul. Ent. Res. 5: 247–249.
5. **Marchand, Werner.** 1917. Notes on the early stages of Chrysops. (Diptera, Tabanidae.) N. Y. Ent. Soc. Jour. 25: 149–163.
6. **Mitzmain, M. B.** 1913. The biology of *Tabanus striatus* Fabricius, the horsefly of the Philippines. Philippine Jour. Sci. 8: 197–221.
7. **Neave, S. A.** 1915. The Tabanidae of southern Nyasaland, with notes on their life histories. Bul. Ent. Res. 5: 287–320.
8. **Schwardt, H. H.** 1930. Notes on the immature stages of Arkansas Tabanidae. Kansas Ent. Soc. Jour. 4: 1–15
9. **Stone, Alan.** 1930. The bionomics of some Tabanidae (Diptera). Ent. Soc. Amer. Ann. 23: 261–304.
10. **Webb, J. L.** and **Wells, R. W.** 1924. Horse-flies: biologies and relation to western agriculture. U. S. D. A. Dept. Bul. 1218, pp. 1–36.

BOOK NOTICE.

A HISTORY OF ENTOMOLOGY. By E. O. Essig. Pages I–VII and 1–1029, 263 figures and portraits. Published by the Macmillan Company, New York, 1931.

This large volume, thoroughly documented and written in great and painstaking detail has a decidedly Pacific Coast slant as is shown by the chapter headings which are as follows: I. Prehistoric Entomology. II. California Indians in Relation to Entomology. III. Historical Background. IV. Principal Institutions in California Featuring Entomology. V. Historical Facts Concerning * * * * * Orchard Mites and Insects of California. VI. Biological Control of Insects. VII. Insecticides. VIII. Entomological Legislation. IX. Biography. X. A Chronological Table Showing Relation to History and Other Sciences. This is a work that every professional entomologist should own. The great amount of historical detail makes it of value as a reference volume but it is so well written that the first eight chapters completely hold the attention of the reader. Chapter IX, which is a series of over one hundred biographies, is more formally written while Chapter X is a table of events in entomology run in parallel with events in world history and in other sciences. The book is a very distinct and outstanding work.—C. H. K.

THE THERMOPILE FOR TEMPERATURE DETERMINATIONS IN ENTOMOLOGY.

WILLIAM ROBINSON.
Chicago, Illinois.

The thermopile, although used in the same way as described for the simple thermocouple*, has the advantage of producing much greater deflections in the galvanometer. This is a very desirable feature at times, especially when a galvanometer of ordinary low sensitivity is used. The thermopile makes it possible to detect very small changes in temperature or to read accurately to .01° or even to .001° C., which is practically impossible with the simple thermocouple.

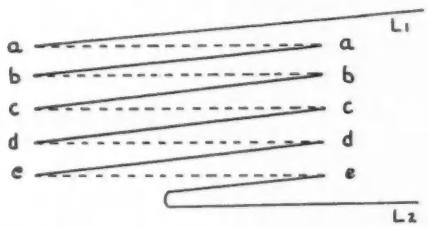


FIG. 1. Arrangement of copper and constantan wires in a thermopile system.

The thermopile is an adaptation of the principle of the thermocouple, and a diagram of its arrangement is shown in Figure No. 1, the full lines representing copper and the broken lines constantan. It will therefore be seen to consist of a number of single couples connected in series. Each single copper-constantan thermocouple develops between 37 and 40 microvolts per degree of temperature difference between its two junctions. Thus, when a number of such couples are connected in series to make a thermopile the total number of microvolts generated will be increased as many times as the number of couples used. The total e.m.f. developed in the thermopile system may, therefore, be comparatively very large depending upon the number of couples.

*The thermocouple method of determining temperature. Ann. Ent. Soc. Am., 20: 513-521; 1927.

The principles of the thermocouple and the potentiometer are described in the previous article referred to; and it is advisable to understand them before proceeding to make and use a thermopile.

CONSTRUCTION OF THE THERMOPILE.

A board is procured about 3 inches greater than the required length of the thermopile, and close to each end a row of small nails is driven in about one-quarter inch apart. There should be 2 nails for each junction plus an extra one at each end for the 2nd lead-in wire. That is, for a thermopile of, say, 10 junctions, 21 nails would be used at each end.

Wire of small diameter such as B. & S. No. 34 gauge is recommended, and double-silk covered insulation is generally preferable, although enamelled wire may have some advantages

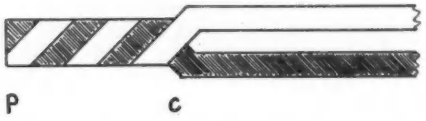


FIG. 2. Spiral connection of wires at junction. Enlarged view.

where the diameter of the bundle of junctions is to be reduced as much as possible. Each odd-numbered nail at one end of the board is connected to the corresponding nail at the other end with a length of copper wire; and each even-numbered nail is connected in a similar manner with constantan. All the wires are then given a coat of shellac to strengthen the insulation and to permit its removal at the tips without fraying. Adequate insulation is important, and at this stage much trouble may be prevented.

When the shellac is dry the wires are fastened down to the board about 6 inches from each end with a strip of adhesive tape. Then with a pair of scissors the wires are cut from the nails.

There are now a number of pairs of copper and constantan wires of equal length lying parallel in preparation for soldering. With a sharp knife the insulation is very carefully removed to expose about 1 inch of metal at each end. This must be done with caution to avoid scraping the metal. Each pair of wires is next connected by twisting together to form a spiral as in

Figure No. 2. The wires must be so joined that a continuous connection of alternate copper and constantan wires is formed with all the junctions in series, as shown in Figure No. 1. These junctions are then soldered, and an electric soldering-iron is preferable as it remains hot while in use. The iron should have a flat surface and upon this some solder is melted. After fluxing, each junction is immersed for an instant in the hot metal which should be deposited in a thin, even covering over the wires.

The points are next cut back to a uniform length of about 2 mm. At this stage it is advisable to test each point to be sure that it constitutes a thermo-electric junction. This is done by connecting to a galvanometer the 2 lead-in wires marked L^1 and L^2 in Figure No. 1, and touching each junction in slow succession with the warm fingers. A deflection indicates that the junction is in effective working condition. This should be done in a room free from sudden changes in temperature, otherwise there may be difficulties in controlling deflections due to variations in temperature of the 2 ends of the thermopile. A good plan is to make up each end of the thermopile into a temporary bundle but bending each junction away from the others so that none are touching. Then place one end in a wide test tube while testing the other end. Precaution should be taken when testing to avoid breathing upon the junctions.

It is important to make each point or junction, shown in Figure No. 2, as short as is consistent with strength. Also when making a determination the points should always be inserted well into the material, otherwise a difference in temperature may exist between C and P and set up secondary thermocouples.

The next step is one that requires especial care, namely, the complete insulating of the exposed metal of each junction. Unless this is done most thoroughly the thermopile will not be satisfactory. For this purpose collodion has been found to give excellent results. Each junction is dipped into collodion well below the exposed metal and allowed to dry thoroughly. A second coat is advisable and a third may be necessary to ensure a complete covering.

After thorough drying for several hours, the junctions at each end are made up into a permament bundle. The points should all have outside positions. This can be done by placing

2 or 3 points at the tip and arranging the others closely together around the sides as in Figure No. 3-a. An effort should be made to reduce the diameter of the warm-junction bundle if it is to be inserted into a small space.

Several methods of finishing the thermopile are available. It may be enclosed in glass tubing, which has some advantages but is too rigid for most purposes in entomology. A satisfactory enclosure can be made with rubber tubing. This does not interfere with flexibility and gives sufficient protection from injury and short circuits. If a momentary lag in temperature determination is permissible, thin glass tubing, sealed at one end, may be used to enclose the bundle of junctions at the "warm" end, as shown in Figure No. 3-b. The bundle is

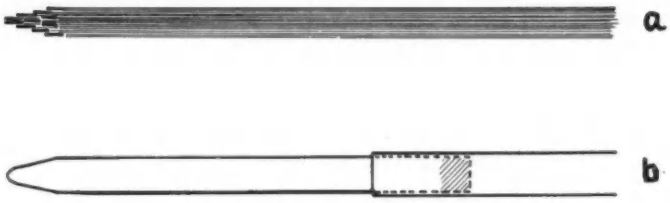


FIG. 3. Arrangement of junctions in bundle; and glass container. Enlarged view.

first dipped in melted paraffin and, while the wax is still soft, is pressed to the tip of the glass tube. This will exclude air and greatly reduce lag. The bore of the tube should be as small as possible. If instantaneous readings are essential the warm junctions should not be enclosed in glass but dipped several times in shellac or other suitable material to protect the collodion insulation. This outer covering should not, of course, be soluble in ether as it would tend to injure the collodion insulation.

The bundle of cold junctions, to be placed in the thermos bottle, should be enclosed in a length of glass tubing sealed at one end, and allowed to rest in the icewater 2 or 3 inches. A convenient exit for the lead-in wires is between the glass and rubber tubing at the cold junction end.

The connection of the thermopile with the potentiometer is similar to that for the simple thermocouple, and is shown

in Figure No. 4. The bundle of junctions at A is the "warm" end and is to be placed in contact with the material of unknown temperature. The "cold" junctions at B are placed in the thermos bottle T. The lead-in wires L^1 and L^2 are connected to the proper binding posts on the potentiometer P. The galvanometer G is used in obtaining the null point.

MAINTENANCE OF THE "COLD JUNCTION" TEMPERATURE.

The temperature indicated by the thermocouple or thermopile is the difference between the temperatures of the thermo-

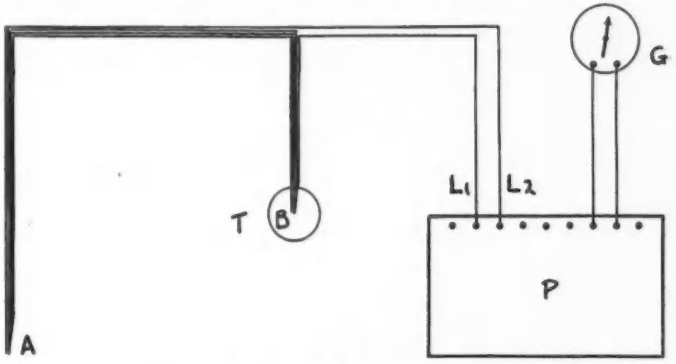


FIG. 4. Showing connections of thermopile with potentiometer and galvanometer.

electric junctions at A and B, Figure No. 4. One of these temperatures, that at B, is required to be known; and the dependability of the couple as a precision instrument can be no greater than the accuracy with which the cold junction temperature is known. The simplest way to satisfy this requirement is to maintain that temperature uniformly constant.

Fortunately a constant temperature can easily be obtained in a suitable mixture of ice and water in a thermos bottle. The bottle should be made up with as much chipped ice from distilled water as it will hold and then be filled up with cold, distilled water. Such a mixture will maintain for hours a temperature in the upper part of the bottle which will not fluctuate from zero more than .001° to .002°. This uniformity

cannot be depended upon unless the thermos bottle is well filled with chipped ice. A bottle half-filled with ice and the remainder with water would produce a temperature gradient as seen in Figure No. 5. This chart shows that the required temperature of zero is obtained only in the upper 2 to 3 inches, below which the temperature is continuously changing. A cold junction resting below the 3 inch level would cause large errors in readings.

When determinations are to be made over long periods of time it is advisable to insert a precision or a Beckmann ther-

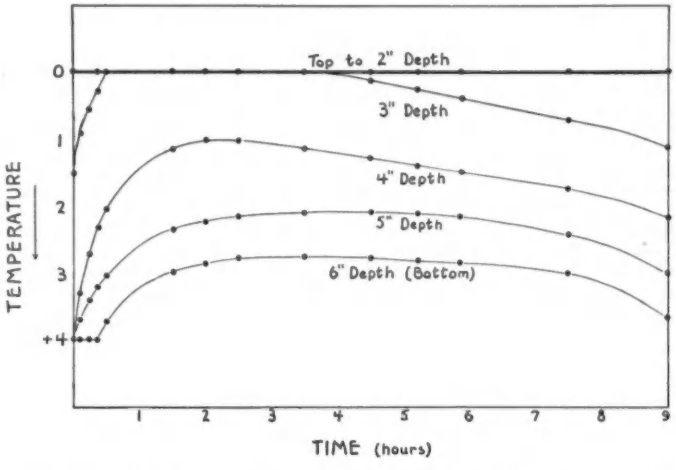


FIG. 5. Showing variations from 0° C. of ice and water in a thermos bottle if insufficient ice is used.

mometer in the cork at the cold junction end, and note when the temperature begins to rise. Both the thermometer and the tube containing the junctions should rest, of course, at the same level in the ice-water.

CALIBRATION.

The number of microvolts which the thermopile will generate per degree of temperature difference now remains to be determined. This value is obtained through the potentiometer. The cold junction is placed in the thermos bottle and the pile is

connected to the potentiometer. The warm junction is next exposed successively to 3 or 4 known temperatures. The number of microvolts generated at each temperature is divided by the number of degrees of temperature between the cold and warm junctions. The results should be practically a constant for all temperatures with which entomologists are concerned. The accuracy with which these various temperatures should be known will depend upon the precision required. If an accuracy in reading within ⅕° or less is satisfactory the pile may be calibrated by the use of water baths, the water being stirred and the thermometer accurate to that extent.

For precision work, temperatures such as transition and melting points are used. The following are suggested:

1. Transition point of manganous chloride..... 58.08° C.
2. Transition point of sodium sulphate..... 32.38
3. Melting point of ice in distilled water..... 0.0

The transition points are easily obtained. For instance, with sodium sulphate, about 20 grams of anhydrous crystals are placed in a clean, wide test tube and moistened with distilled water. The temperature of the mass will then rise to 32.38° C. The warm junctions should be pushed well in, and when the temperature ceases to rise and remains constant for a time the number of microvolts generated should be noted. That value divided by 32.38 will give the number sought.

In all subsequent work, for assurance that the thermopile and its accessory apparatus are in reliable working condition, a daily check-up with some known temperature is recommended.

HOW TO APPLY THE CONSTANT OBTAINED BY CALIBRATION.

Having determined the number of microvolts, C, which the thermopile will generate per degree of temperature difference, any unknown temperature may be read by dividing the number of microvolts generated by the constant C. The value for C will be reliable to about 0.01° through the range of temperatures used in calibration and probably for all temperatures in which entomologists are interested.

IMPORTANCE OF THE SEX RATIO IN ORIENTAL FRUIT MOTH PARASITE BREEDING.*

PHILIP GARMAN AND J. C. SCHREAD.

Parasite breeding under artificial conditions is beset with many pitfalls in which the unwary may come to grief. Among those worth mentioning are the maintenance of host material in sufficient numbers, the provision of suitable quarters for the parasites to work, and finally the provision of parasites and hosts in a continuous succession, as well as the maintenance of an ever increasing parasite population so that some may be laid aside for distribution or liberation. In connection with

TABLE I.

Per Cent of Males of *Macrocentrus ancylivora* Roh. Reared at Different Times under Different Conditions.

SOURCE OF PARASITE MATERIAL	TOTAL PARASITES	PER CENT MALES
Collected in New Jersey in June and July	9,590	41.0
Reared in:		
July—Insectary	1,936	48.6
August—Insectary	1,063	68.5
September—Greenhouse	686	69.2
October—Greenhouse	1,599	69.5
November 1-10—Greenhouse	138	68.8
November 11-30—Greenhouse	142	53.1

the latter problem it has become increasingly apparent that the sex ratio of the parasite is one of the limiting factors in maintaining a sufficient increase to keep ahead of the game. It has generally been accepted that the ratio of males and females is constant, a few writers, however, indicating the effects of temperature on the ratio. The data which we present herewith bear upon this problem in showing that it is an easily variable ratio, affected strongly by refrigeration in the case of *Trichogramma*, Table II, and possibly by several factors for *Macrocentrus*. It will be seen that the percentage of male *Trichogramma* emerging after 12 days refrigeration was 25 per

*Contribution from the Com. Agr. Exp. Station, 1931.

cent, whereas the percentage was 75 after 50 days. In the case of *Macrocentrus* (Table I) it will be seen that the percentage of males varies all the way from 41 per cent for material imported from New Jersey to 69 per cent for parasites reared in September under greenhouse conditions.

It has been our experience that *Trichogramma* quickly come back to a low percentage of males, which is indicated by the last two items in Table II, the results of continuous generations

TABLE II.

Effect of Refrigeration on Percentage of Male *Trichogramma minutum* Riley.†

EXPOSURE IN REFRIGERATOR AT 38–40–° F, DAYS	PER CENT OF EGGS HATCHED	PER CENT MALES EMERGING	NOTES
12	67	25	
23	46	34	
24	20	40	
26	40	61	
28	51	52	
33	46	67	
41	20	66	
43	19	66	
44	23	66	
45	12	76	
50	17	76	
54	6	69	
62	2	77	
None	94	33	Continuous rearing without intervening refrigeration.
None	92	25	

†Reared in eggs of *Sitotroga cerealella* Oliv.

after removal from the refrigerator. Normally it requires three to four generations for *Trichogramma* to regain their usual reproductive power after long exposure to cold.

In the case of *Macrocentrus* it is not difficult to figure mathematically the difference in the rate of increase for those with high and low percentages of males. Thus if we start with an initial number of 10 adult parasites of which seven are males, (allowing six eggs for each female and assuming a constant ratio as occurred from August to October) in four generations there will be 102 adults of which 30 are females. If, on the other hand, the ratio of males to females is equal, there will result in four generations 710 adults, of which 355

are females, or, if the ratio of males is still lower, approximately two-fifths of the whole as occurred with the *Macrocentrus* collected from New Jersey, there will be 1675 adults, or 1005 females, at the end of the fourth generation. Thus instead of 30 female parasites after four months (average life cycle 28 days, preoviposition period, three days) the operator would theoretically at least have more than 30 times as many. While this difference is not always attainable in breeding work, the importance of this factor cannot be ignored and should, we believe, be carefully considered in the mass production of any parasite. It likewise seems probable that there is considerable fluctuation in the normal ratio in the field for if a change of ratio is so easily produced, there must be a considerable difference in different localities and climates, which may even affect abundance or natural distribution.

BOOK NOTICE

DEMONS OF THE DUST. By WILLIAM MORTON WHEELER, W. W. Norton & Company, Inc., Publishers, New York.

This book is not, as might be imagined from the title, a tale of bull fights in Mexico, or cowboy adventures on the plains, nor even of auto racers on the sands of Daytona beach. However the title will be found quite fitting as Doctor Wheeler has brought together in this book a very interesting collection of studies upon certain groups of insects which have developed diabolical habits in securing their food.

There is an interesting chapter on "Some Eighteenth Century Naturalists," treating of certain writers who presented the results of their studies of these insects; a chapter on "The Fauna of the Sands," giving a general survey of adaptation to arid conditions, then a series of chapters reviewing studies of different dust or sand inhabiting species with a quite complete monograph of the genus Lampromyia. Appendices include translations of early papers by De Geer and Reaumur. There is an extended and very complete bibliography.

This book is written in Doctor Wheeler's very interesting style and the illustrations and descriptions are evidently of his usual exact and illuminating portraiture. The book will appeal to a wide circle of readers, both on account of its entertaining style and the remarkable habits of the insects treated. To students of entomology it offers both a comprehensive discussion of certain insects and a model of presentation for complex biological phenomena.—H. O.

NEW ASILIDÆ, WITH A REVISED KEY TO THE GENUS STENOPOGON LOEW: (DIPTERA).

STANLEY W. BROMLEY,
Bartlett Tree Research Laboratories,
Stamford, Connecticut.

The species dealt with in the present paper were in the collection of the late Professor James S. Hine, of the Ohio State Museum, Columbus, Ohio. In several instances the specimens had been set apart, evidently for description in the future. Unfortunately death intervened and this desired result was not obtained. It has been a privilege accorded me to study the remarkable collection which Professor Hine left and the present notes are the results of a preliminary survey of this collection.

The types of the new species are in the Hine Collection. Ten species, representing three subfamilies, are described.

DASYPOGONINÆ.

The genus *Stenopogon* Loew has been treated by Back in his excellent work on the Robberflies of America, North of Mexico, belonging to the Subfamilies Leptogastrinæ and Dasypogoninæ (Transactions of the American Entomological Society, XXXV, 1909, pages 137–400, 11 plates). This key is herewith presented in a revised form to accommodate the new species described.

KEY TO STENOPOGON LOEW.

1. Katapleurotergite ("Hypopleura") bare 2
   Katapleurotergite ("Hypopleura") with hair or bristles (*Scleropogon*).... 13
2. Third segment of antenna somewhat oval, arista short and bristle-like, wings short and narrow 3
   Third segment slender, arista not so sharply differentiated, wings longer and broader 5
3. Species 15–19 mm. in length, vestiture of thoracic dorsum yellowish, posterior portion unusually bristly ..... **breviusculus** Loew.
   Small, slender species (10–13 mm. in length), vestiture finer and more scanty 4
4. Black species ..... **nigritulus** Coquillet
   Yellowish-brown species ..... **albibasis** Bigot
5. Sternopleura with a tuft of long fine pile 6
   Sternopleura without such a tuft, although usually with some pile 12
6. Mystax black ..... **jubatus** Coquillet
   Mystax lighter-colored 7

7. Abdomen black, at least first five segments 8
Abdomen with varying amounts of reddish on these segments 10
8. Reddish pollinose, vestiture of head mostly reddish-yellow ..**rufibarbis** n. sp.
Grayish-yellow pollinose, vestiture of head straw-colored 9
9. Robust species, base of abdomen and thorax rather thickly straw-yellow pilose ..... **felis** n. sp.
Less robust species; base of abdomen and thorax not as thickly pilose, **obscuriventris** Loew.
10. Robust, reddish-haired in male; female with vestiture more straw-colored; abdomen partly reddish above, sides broadly black ..... **gratus** Loew
11. More slender, vestiture straw-colored; abdomen mostly reddish, sides narrowly black ..... **californiæ** Walker
12. Large variable species (20–37 mm.) with varying amounts of red on abdomen ..... **inquinatus** Loew
(= *modestus* Loew)
(= *morosus* Loew)
13. Third segment of antennae elongate, style usually short, sometimes longer and more slender, first posterior cell generally open 14
Third antennal segment more oval, style bristle-like; first posterior cell more frequently closed 21
14. Decidedly black, with or without red on abdomen; the latter not obscured by a grayish bloom; wings black 15
Reddish; or if black, with abdomen obscured by bloom; wings reddish or brownish 16
15. Abdomen wholly polished black ..... **nitens** Coquillet
Abdomen, except base and tip, reddish ..... **aecidinus** Williston
16. Southeastern species; reddish-yellow, abdomen long and quite slender, wings broad, dark brownish ..... **subulatus** Wied.
Western species 17
17. Abdomen unusually long; wings long and narrow, yellowish-gray; (abdomen, except back and sides, reddish) ..... **longulus** Loew
Abdomen less elongate, wings shorter and usually broader 18
18. Blackish, covered uniformly with grayish bloom ..... **pumilus** Coquillet
Reddish (abdomen at least) 19
19. Wings brownish with considerable reddish toward base 20
Wings darker, no reddish; large, robust species (22 mm.) (Texas), **tenebrosus** Coquillet
20. Thorax grayish pruinose; bristles whitish ..... **consanguineus** Loew
Thorax yellowish pruinose; larger and more robust; wings broader, femora stouter; bristles of body more golden, (Texas) ..... **latipennis** Loew
21. First posterior cell closed 22
First posterior cell open 25
22. Wholly and densely grayish white pruinose, wings hyaline; small (15 mm.) slender species ..... **cinerascens** Back
Not completely and densely whitish pruinose 23
23. Large species (20–28 mm.) 24
Smaller species (15–19 mm.); thorax grayish-yellow pollinose, contrasting with abdomen which is gray pollinose ..... **coyote** n. sp.
24. Chamois-leather yellow, abdomen long and slender, without black fasciae ..... **helvolus** Loew
Yellowish-gray pruinose, abdominal segments black with posterior margins and venter red ..... **picticornis** Loew
25. Reddish species with black margins on thorax; wings blackish with reddish toward base ..... **texanus** n. sp.
Black species, grayish pollinose; wings hyaline ..... **neglectus** n. sp.

Stenopogon coyote, new species.

Total length, 15–19 mm. Resembles a miniature *S. helvolus* Loew. The hypopleura bear fine hairs, the arista is bristle-like, the first posterior cell is closed as in *helvolus*, but the ground color of the body is black. The pollen of the abdomen is more grayish than that of the thorax where it is grayish-yellow, making a slight contrast between the color appearance of the two regions.

Male.—Proboscis and palpi dark reddish-brown; 1st 2 antennal segments reddish-yellow, third and arista black. Vestiture of head straw-yellow, darkest on vertex; the beard lightest. Thorax black, covered with a grayish-yellow bloom, vestiture straw-yellow. Humeri and a small area just beneath reddish. Wings hyaline, short as in *helvolus*. Legs reddish, femora black above. Hind tibiæ darker than others. Hairs and bristles of legs straw-colored. Abdomen black, grayish pollinose, and covered with fine straw-colored hairs. There is a suggestion of reddish at the incisures and the genitalia are reddish.

Female.—Similar, the ovipositor with dark reddish-brown bristles.

Holotype, ♂, near Lander, Wyoming, 5000–8000 feet, July (Roy Moodie). *Allotopotype*, ♀, same data. *Paratopotype*, ♀. *Paratypes*, ♂♂ (2), 40 miles north of Lusk, Wyoming, July, 1895; Salida, Colorado, July 16, 1898; Poncha Springs, Colorado, July 13, 1898. ♀♀ (4) 40 miles north of Lusk, Wyoming, July, 1895; Las Cruces, New Mexico, May (Cockerell); Garden of the Gods, Colorado City, Colorado, July, (E. S. Tucker); Flagstaff, Arizona, June 4; Salida, Colorado, July 16, 1898; Poncha Springs, Colorado, July 7, 1898.

The venter of the abdomen varies from reddish to black. This seems to be a common species in collections and one frequently identified as *S. helvolus* Loew. It is however definitely distinct from that species.

Stenopogon felis, new species.

Total length, 22–24 mm. Similar to *S. obscuriventris* Loew., but differs in having the abdomen more thickly pilose toward the base, all the tibiæ being blackish toward the tip, and in being somewhat more robust in general appearance.

Male.—Black; vestiture of head pale yellowish, the beard and palpal hairs lighter. A few black hairs on vertex. Head and thorax grayish-yellow pollinose. Hairs and bristles of mesonotum pale yellow, black hairs along median line. Pleural and coxal hairs and hairs and bristles of legs pale yellow. Basal ⅕ths of femora, tips of tibiæ and tips of tarsomeres of posterior tarsi black, rest of legs reddish-yellow. Wings pale brownish, anal angle milky-white, base of veins reddish. Halteres pale brown. Abdomen shining black, incisures dark brown;

thickly covered with fine golden pile which is longer and thicker toward the base. Genitalia black with golden hair.

Female.—Similar, but without milky-white anal angles of the wings. Spines of ovipositor dark reddish.

Holotype, ♂, Coronado, California, June 22, 1890. (F. E. Blaisdell). *Allotopotype*, ♀, same data.

Stenopogon neglectus, new species.

Total length, 19-28 mm. A black species, dark gray pollinose, related to *Stenopogon* (*Scleropogon*) *helvolus* Loew, but differing in having the first posterior cell open, and in being black in ground color with a dark grayish bloom, instead of chamois-yellow with a grayish-yellow bloom. The incisures of the abdomen are brownish. Antennal style bristle-like. "Hypopleura" with fine hair.

Male.—Antennæ, proboscis and palpi black. Face and occiput silvery pruinose. Vestiture of beard very pale straw-colored, beard nearly white. Thorax black, except the humeri, a small area just beneath humeri, and areas along the sutures of the pleura, which are reddish. Front coxæ black, others reddish with black areas anteriorly. Thoracic vestiture straw-colored, except fine hairs on mesonotum which are black. Thorax with grayish bloom. Legs with straw-colored bristles and hairs. Middle and posterior femora black above, reddish-below. Tibiæ light reddish-brown, the hind almost black. Tarsi light reddish brown. Wings short as in *helvolus*, nearly hyaline, first posterior cell open. Abdomen black, gray pollinose, with fine straw-colored hairs. Venter and margins of segments pale reddish-brown. Genitalia reddish-brown below, blackish above.

Female.—Similar; margins of abdominal segments more narrowly reddish. A reddish dorsal line on segments 7 and 8. Spines of ovipositor reddish.

Holotype, ♂, near Lander, Wyoming, 5000–8000 feet, August (Roy Moodie). *Allotopotype*, ♀, same data. *Paratopotypes*, 5 ♂♂; ♀♀2. *Paratypes*, ♂♂ (4), Lewiston, Idaho; (2) Creeds, Colorado, 8844 feet, August, 1914 (S. J. Hunter); Yellowstone Park, July 25, 1923, Roaring Mountain [elevation, 7500 feet] (H. C. Severin); ♀♀, Lewiston, Idaho; Creeds, Colorado, 8844 feet, August 14 (S. J. Hunter); Castle, Oregon, September 2, 1923 (Carl Duncan); Ac. SL. Dsrt, Utah, July 24, 1925 (Hall).

The width of the reddish margins on the abdominal segments varies considerably as does the color of the venter; in some the venter is darker, almost black. In one anomalous specimen the first posterior cell is closed in one wing and open in the other. In some of the males, the genitalia are entirely black.

Stenopogon rufibarbis, new species.

Total length, 20–23 mm. Related to *obscuriventris* Loew, from which it may be distinguished by the brighter, more reddish color of the legs, the vestiture of the head and abdomen, the pollen of the thorax; and to *gratus* Loew from which it may be separated by the uniform color of the hind tibiæ, lacking the darkened apex of *gratus*, and the absence of red areas on the dorsum of the abdomen.

Male.—Black. Vestiture of head light reddish, except hairs on vertex which are black. Head and thorax brassy-yellow pollinose, inclined to reddish on thorax. Mesonotum with black hairs, the posterior portion and the scutellum with reddish bristles. Pronotum and pleura with pale reddish hairs. Wings tinged with brownish, the anal angles milky-white. Bases of veins reddish. Halteres pale reddish. Coxæ and legs with reddish hairs and bristles. Tarsi, tibiæ and distal fifth of femora reddish; rest of femora black. Abdomen shining black with pale reddish or golden pile. Genitalia reddish.

Female.—Similar, but with the wings uniformly brownish, the first 5 segments of abdomen grayish brown pollinose, the succeeding shining black; 7th tergite reddish.

Holotype, ♂, Lassen Co., California, July 20, 1911. *Allotype*, ♀, San Antonia Canyon, Ontario, California, July 25, 1907. *Paratypes*, ♂♂ (3) Lassen Co., California, July 20, 1911; ♀♀ (3) Lassen Co., California, July 20, 1911; Los Angeles Co., California, 1200 feet, near Pasadena, May 5, 1910 (F. Grinnel, Jr.); "Cala." (no other data).

Some of the males have the genitalia blackish, and some of the females have the 7th tergite in addition to the 8th reddish, but none have the reddish areas on the preceding segments as occurs in *gratus* Loew and *californiæ* Walker.

Stenopogon texanus, new species.

Total length, 18–23 mm. A handsome reddish species with wings reddish towards base and along anterior margin, brownish elsewhere; black markings on the mesonotum; the hypopleura with fine hair, the style of antennæ short and the first posterior cell open.

Male.—Reddish. Head black, the face grayish-white pollinose, the occiput golden pollinose. Antennæ reddish with black bristles; proboscis black, mystax, palpal hairs and beard pale yellowish-white. Occipital bristles golden; hairs of vertex black. Prothoracic bristles pale reddish. Thorax red; pleura and coxæ partly blackish. The mesonotum bears three black lines, the median narrowly bisected longitudinally, with a golden streak of pollen. Sides of mesonotum also golden pollinose. Hairs and bristles of mesonotum black, except those of humeral callus which are reddish. Pleura and coxæ with pale golden hairs. Legs reddish with concolorous hairs and black

bristles. Middle and posterior femora with a black line on upper surface, front femora with a black streak anteriorly and another posteriorly. Many fine hairs on the dark streaks black. Wings brownish toward tips, bases and anterior margin reddish. Scutellum reddish with a black spot at base; bristles black. Halteres pale yellowish-brown. Abdomen reddish, blackish at ends, the dark areas covered with grayish bloom; with fine scattered reddish hairs. Genitalia reddish with black hairs. Venter reddish.

Female.—Similar, but with some pale bristles in posterior part of mesonotum. Abdomen darker towards tip.

Holotype, ♂, Dilley, Texas, May 6, 1920 (H. J. Reinhard). *Allotopotype*, ♀, May 5, 1920 (H. J. Reinhard). *Paratypes*, ♂, Marble Falls, Texas, April 4, 1923 (C. A. Harned); ♀ ♀, Marble Falls, Texas, April 21, 1923 (C. A. Harned); Christoval, Texas, April 27, 1915 (A. K. Fisher).

Heteropogon rubrifasciatus, new species.

Total length, 10–15 mm. A black species related to *macerinus* Walker, but differing in having the posterior margins of abdominal segments 2-6 reddish and 7th segment entirely so. The middle tibiæ in the male lack the brush of black hairs and bristles characteristic of *macerinus*.

Male.—Head pilose and bristles, the vestiture whitish, except the following which are black; a few bristles on antennæ, vertex and occiput and the palpal hairs. Antennæ and proboscis dark brown. Thorax grayish pollinose, with three broad blackish stripes on the mesonotum. Hairs on notum mostly black, but the thick pile on the pronotum and pleura is whitish. Some of the bristles on the posterior portion of the mesonotum and on the scutellum are white. Legs dark reddish brown with black bristles and fine white hairs. Wings very faintly tinged with brown, slightly darker along the anterior portion of the apical half. The wings are noticeably clearer than those of *macerinus* Walker. Halteres reddish brown.

Abdomen black with pale yellowish-white pile. Posterior margins of segments 2-6, broadly reddish, the sixth mostly and the 7th entirely red. There is a whitish spot on the posterior lateral margins of segments 1-4. Genitalia reddish, the bases of the upper forceps dark reddish-brown.

Female.—Similar, but with wings slightly darker. Segments 5 and 6 are mostly reddish above, blackish at sides, while the following are black. Spines on ovipositor black.

Holotype, ♂, Southern Pines, N. C., September 12, 1912 (A. H. Mennee) (No. 11). *Allotopotype*, ♀, same data, No. 12. *Paratopotypes*, ♂, September 12, 1912 (A. H. Mannee). (Note by H. S. Harbeck, "Heteropogon near *gibbus*, probably new");

♀ ♀, September 3, 1912; September 28, 1915; September 28, 1915 (label, "Preys from tips of dead twigs"). All collected by A. H. Mannee and in the J. S. Hine collection.

Deromyia neoternata, new species.

Total length 18–29 mm. A pale reddish species with three velvety black stripes on the mesonotum; the abdomen without black spots on the sides of the segments, coarctate, the constriction coming between the second and third segments. This species has been hitherto known as *ternata* Loew, a cuban species which differs in several respects as I pointed out in the Asilidæ of Cuba (Annals Ent. Soc. Amer. Vol. XXII (1929) p. 278.) *Neoternata* differs from *ternata* as follows: it is proportionately less robust, the pollen on the thorax is less decidedly golden, the median line on the mesonotum fades into reddish anteriorly, and there is no blackish area above the second and third coxæ.

Holotype, ♂, Russell Co., Kansas, 1830 feet, August 26, 1912. (Coll. F. X. Williams). *Allotype*, ♀, Osborne Co., Kansas, 1557 feet, August 3, 1912 (F. X. Williams).

I have examined numerous specimens from Florida to Colorado and from Indiana to Texas. I have collected the species in Missouri, South Carolina, and Indiana. It occurs mostly where the herbage is rank at the edge of low fields or woods and many of the specimens I have collected were noted in and around blackberry or raspberry thickets.

LAPHRIINÆ.

Laphria stygia, new species.

Total length 25–27 mm. A large black species with small whitish pruinose spots on the posterior lateral margins of abdominal segments 2-4, inclusive. The wings are black and there are bluish or purplish reflections on the thorax and abdomen.

Female.—Head black; vestiture coarse, black; a very small tuft of whitish hairs under the eyes and a few minute scattered white hairs on the face. Face, vertex (except ocellar tubercle), and occiput near margin of eyes thinly brownish pollinose. Thorax black with black hairs and bristles. Ground color of mesonotum deep metallic blue. Hairs and stiff marginal bristles of scutellum black. Pleura light brown pollinose, becoming almost silvery near coxæ. Wings black or very dark brown, the interior of some of the larger cells paler. Halteres light brown. Legs and abdomen black with deep metallic bluish reflections. Hairs and bristles, stout, black. The posterior lateral margins of segments 2-4 (inclusive) whitish pollinose. Ovipositor short as in *Laphria*, with a few long black bristles.

Holotype, ♀, Stovall, North Carolina, June 26, 1919, (J. A. Eckert). *Paratypes*, ♀ ♀, Ovett, Mississippi, June 20, 1914 (J. W. Hathaway); June, 1916, Locality (?).

This species would fall in the genus *Laphria* if the old definition were adhered to. The proboscis is, however, of an entirely different type from the typical Laphria, but approaches that of *Panamasilus* Curran. The species appears to be confined to Southeastern United States and is undoubtedly very rare. It superficially resembles *Pogonosoma dorsatum* vr. *melanopterum* Wied., but a comparison of the two shows them to be entirely unrelated.

Bombomina engelhardti, new species.

Total length 17-23 mm. A yellow pilose species, with the scutellum and first segment of the abdomen with black hairs and bristles. There is considerable reddish pile mingled with the yellow pile on the abdomen. Related to *B. fernaldi* Back, from which it may be distinguished by the even distribution of the red hair on the abdomen, not restricted to certain areas as in *fernaldi*, and the first segment of the abdomen being always black-haired in contrast to the second which is thickly yellow pilose.

Male.—Head black, yellow pilose, except hairs of upper part of occiput, and a few hairs in lower part of mystax, beard, and on palpi which are black. Pronotum with black bristles. Mesonotum thickly dark yellow pilose. A yellow tuft of hairs in front of wings and in front of halteres. Coxæ yellow-haired; considerable black on posterior pair. Legs black with black hairs, except the hairs on posterior aspect of front femora, the dorsal aspect of the first and second pair of tibiæ, and a few hairs on the dorsal aspect of the basal portion of the hind tibiæ, which are yellow. Wings and halteres light brownish. Scutellum and first segment of abdomen with black hairs and bristles. Segments 2-6 above densely yellow pilose with reddish hairs uniformly intermingled. Genitalia black or with some black and some pale hairs and bristles.

Female.—Similar, except black hairs predominate in beard and on coxæ. The apex of the abdomen from the 7th segment on is black-haired, with a few yellowish hairs on ovipositor.

Holotype, ♂, S. W. Colorado, July 15, 1898. *Allotype*, ♀, Jemez Springs, New Mexico, May 24, 1913 (John Woodgate). *Paratypes*, ♂ ♂ (6) Jemez Springs Mountains, New Mexico; (2) Oak Creek Canyon, Arizona, 6000 feet, August (F. H. Snow); "Colo." ♀ ♀ (3) Jemez Springs Mountains, New Mexico; S. Arizona (F. H. Snow), August, 1902. S. Franc Mountain, Arizona, July 15 and July 14, 1892; Durango, Colorado, June 14, 1889.

Named in honor of Mr. G. P. Engelhardt, who collected this species in New Mexico.

ASILINÆ.

Promachus hinei, new species.

Total length, 30–35 mm. Closely related to *Promachus rufipes* Fabr. from which it may be distinguished by the femora being reddish instead of black, the light pollen of the abdomen grayish or grayish yellow instead of yellow; the thorax deeper reddish brown, and the pale pile of the head thorax and abdomen grayish instead of yellow.

This is the species referred to by Hine, (Annals Ent. Soc. America, Vol. IV, (1911), p. 166,) under *Promachus rufipes* Fabricius. *P. rufipes* Fabricius occurs for the most part east of the Alleghanies, while *hinei* n. sp. occurs west of the Alleghanies from Ohio to Texas and Missouri. The specimen figured under the name *vertebratus* in Howard's Insect Book, Plate XVIII, Fig. 8, is *hinei*. Both *rufipes* and *hinei* occur in Ohio.

Holotype, ♂, West Jefferson, Ohio, August 26, 1923. *Allotopotype*, ♀, same data. *Paratypes*, ♂ ♂, Georgesville, Ohio, September 10, 1898; Posey Co., Indiana, August 10, 1924; Benoit, Mississippi, July 18, 1899; Henry County, Iowa, August 25, 1904; C. T. Vorhies; ♀ ♀, Oxford, Ohio, Coll. W. H. S.; Victoria, Texas, August 1, 1925. R. H. Painter Coll., another same data with a Megachilid bee as prey; Geneva, Indiana, August 6, 1911 (E. B. Williamson Coll.) with an Andrenid bee as prey.

Named in honor of the late Professor James S. Hine, who had worked extensively on the North American species of this genus of *Asilidæ*.

NOTES ON THE BIOLOGY OF THE STABLE-FLY, STOMOXYS CALCITRANS LINN.

ROY MELVIN,
Zoology and Entomology Department, Iowa State College,
Ames, Iowa.

A review of the literature pertaining to the Stable-fly, *Stomoxys calcitrans* Linn., revealed the fact that our knowledge of the life history of this important stock pest under constant temperature and humidity conditions was far from complete. In the course of an investigation which necessitated the rearing of large numbers of *S. calcitrans*., a few notes on the life history of this insect were made which seem worthy of a brief presentation.

Incubation Period. At 20 minute intervals eggs were removed from test tubes containing gravid female *S. calcitrans*, and placed on wetted toweling paper in small ground glass top stender dishes. The stender dishes were then placed in constant temperature ovens. When hatching commenced, the larvæ were removed and the number recorded at 20 minute intervals. The results of these studies were as follows:

Temperature, °C.	Number of Observations	Range	Mean Time in Hours
25	1169	32.5–35.2	33.4
30	1264	25.0–28.5	26.5

Larval and Pupal Period. The length of the larval period was determined indirectly, e. g.: The larval and pupal periods were determined together and then the pupal period was determined separately. For rearing the larvæ two types of containers were employed, namely: 2-oz., wide-mouth bottles for groups of 10 larvæ, and battery jars, 15.5 cm. in diameter and 20.5 cm. high, for groups of 100 larvæ.

Newly hatched larvæ were placed upon the breeding media (See Table I) and observations made every two hours during time of emergence. Table I shows the results of these tests.

Numerous rather unsuccessful attempts were made to rear *S. calcitrans* on both clean wheat straw that had been wetted down for 1, 2, 5, 10, and 20 days, before the larvæ were placed

TABLE I.

Showing Effects of Food and Temperature on Length of Larval and Pupal Periods of *S. calcitrans*.

Temp. °C.	Container	Breeding Media	No. Observations	Hour Range	Mean Time in Hours
25	2-oz. bottles...	Wheat bran and alfalfa meal, half and half by weight.....	278	351–406	377
25	Battery jar....	Wheat bran and alfalfa meal, half and half, by weight.....	81	337–409	372.6
30	2-oz. bottles...	Wheat bran and alfalfa meal, half and half, by weight.....	798	293–349	311.7
30	Battery jar....	Ground oats.....	178	304–344	320.2
30*	Battery jar....	Ground oats.....	303	297–347	326.1

*Results of preliminary test made during summer of 1929.

TABLE II.

Showing Effect of Various Relative Humidities on the Per Cent Emergence and Length of Pupal Stage of *Stomoxys calcitrans* Linn, at 25° C.

Salt	Approx. Per Cent R. H.	Number Pupa Started	Per Cent Adults	Length of Pupal Period	
				Range	Mean Time in Hours
H^2O.....	100	575	99.8	168–192	177.2
NaCl.....	73	100	10	140–189	164.6
$KC^2H^3O^2$.....	19	50	0	.....	.....
H^2SO^4 Conct....	0	200	0	.....	.....

thereon and clean wheat straw which had been steam cooked at 90° C. under about ten pounds pressure for 1, 2, 4, 12, and 24 hours. The per cent emergence was less than 10 in all

of the above mentioned cases, and the individuals appeared to be invariably smaller than those reared from ground oats or wheat bran and alfalfa meal.

Pupal Period. Newly formed white pupa were removed from the breeding media and placed at constant temperature and constant relative humidities. Observations were made every two hours during time of emergence. Table II shows the results of these tests.

SUMMARY.

From the data presented above the following conclusions are drawn:

I. Incubation period of *S. calcitrans* at 25° C. is 33.4 hours; at 30° C., 26.5 hours.

II. Larval and pupal period of *S. calcitrans* breed on alfalfa meal and wheat bran half and half by weight at 25° C., was 377 hours; at 30° C., 311.7.

III. Larval and pupal periods of *S. calcitrans* breed on ground oats at 30° C. was 320.2 hours in one series of tests and 326.1 hours in another series of tests.

IV. Pupal period of *S. calcitrans* at 100%. R. H. was 177.2 hours.

V. Only 10% adults were obtained from pupa placed over a saturated solution of NaCl, approximately 73% relative humidity at 25° C.

BOOK NOTICE

GUIDE TO THE STUDY OF THE WINGS OF INSECTS. By JAMES CHESTER BRADLEY. Pages 1–41, plates 1–67, (unbound). Published by Daw, Illston and Company, Ithaca, New York.

This is a paper-bound classroom manual accompanied by sixty-seven loose plates on each of which is printed, in scarcely visible ink, the wing of an insect, which is to be traced and lettered in india ink by the student. The nomenclature is that of the Comstock-Needham system with the modifications of the M-Cu region necessitated by the recent researches of Lameere, Tillyard and Martynov.

The editor feels that there should be a set of plates (a key or "pony") with the veins properly marked which could be used for reference by the teacher. At the end of the booklet are comparative tables showing the relation of this system to previously used systems. This is an excellent method of teaching venation.—C. H. K.